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Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates

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ABSTRACT

Soil organisms drive major ecosystem functions by mineralising carbon and releasing nutrients during decomposition processes, which supports plant growth, aboveground biodiversity and, ultimately, human nutrition. Soil ecologists often operate with functional groups to infer the effects of individual taxa on ecosystem functions and services. Simultaneous assessment of the functional roles of multiple taxa is possible using food-web reconstructions, but our knowledge of the feeding habits of many taxa is insufficient and often based on limited evidence. Over the last two decades, molecular, biochemical and isotopic tools have improved our understanding of the feeding habits of various soil organisms, yet this knowledge is still to be synthesised into a common functional framework. Here, we provide a comprehensive review of the feeding habits of consumers in soil, including protists, micro-, meso- and macrofauna (invertebrates), and soil-associated vertebrates. We have integrated existing functional group classifications with findings gained with novel methods and compiled an overarching classification across taxa focusing on key universal traits such as food resource preferences, body masses, microhabitat specialisation, protection and hunting mechanisms. Our summary highlights various strands of evidence that many functional groups commonly used in soil ecology and food-web models are feeding on

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multiple types of food resources. In many cases, omnivory is observed down to the species level of taxonomic resolution, challenging realism of traditional soil food-web models based on distinct resource-based energy channels. Novel methods, such as stable isotope, fatty acid and DNA gut content analyses, have revealed previously hidden facets of trophic relationships of soil consumers, such as food assimilation, multichannel feeding across trophic levels, hidden trophic niche differentiation and the importance of alternative food/prey, as well as energy transfers across ecosystem compartments. Wider adoption of such tools and the development of open interoperable platforms that assemble morphological, ecological and trophic data as traits of soil taxa will enable the refinement and expansion of the multifunctional classification of consumers in soil. The compiled multifunctional classification of soil-associated consumers will serve as a reference for ecologists working with biodiversity changes and biodiversity–ecosystem functioning relationships, making soil food-web research more accessible and reproducible.

Key words: soil food web, soil fauna, food resources, omnivory, feeding preferences, trophic guilds, functional traits, stable isotopes, fatty acids, gut content

CONTENTS

I. INTRODUCTION

(1) Belowground consumers and ecosystem functioning

Biota play an important and active role in soil, supporting elemental cycles and shaping overall ecological and evolutionary responses of terrestrial ecosystems to environmental changes (Bardgett & van der Putten, 2014; Crowther *et al.*, 2019). Soil communities comprise prokaryotes and fungi, which release enzymes into the environment for food digestion, and heterotrophic protists and animals (hereafter termed 'consumers' for simplicity), which ingest food resources from the environment and digest them inside their body. Together, they form the decomposer system responsible for fundamental ecosystem functions such as decomposition of organic matter, nutrient release, soil aggregation and plant growth, and supporting aboveground food webs (Lavelle, 1996; Bardgett, Hopkins & Usher, 2005; Wagg *et al.*, 2014; Steffan & Dharampal, 2018). Soils host about 50% of global animal biomass (Fierer *et al.*, 2009) and the majority of terrestrial animal biodiversity is associated with soil and litter as a habitat or food source (Table 1). Nevertheless, while soil prokaryotes and fungi are recognised as important drivers of ecosystem functions in biogeochemical models, soil protists and animals are often neglected (Filser *et al.*, 2016; Deckmyn *et al.*, 2020). This is surprising considering that consumer communities can strongly affect decomposition (García-Palacios *et al.*, 2013), soil structure (Jones, Lawton & Shachak, 1994), plant nutrition (Bonkowski, 2004) and functional responses of microbial communities (Crowther *et al.*, 2015; Thakur & Geisen, 2019). The magnitude and direction of these effects depend on the particular consumer type and its interactions with other biota and the environment (Bradford *et al.*, 2002; Hättenschwiler, Tiunov & Scheu, 2005; Eisenhauer, Reich & Isbell, 2012; Coulibaly *et al.*, 2019). To assess ecosystem-level effects of different belowground consumers, a number of functional classifications has been suggested for individual taxonomic groups (Gisin, 1943; Bouché, 1977; Ferris, Bongers & De Goede, 2001). However, these classifications were developed independently from each other and have to date not been synthesised into a common system across the variety of consumers including protists, microfaunal, mesofaunal and macrofaunal invertebrates as well as vertebrates associated with soil.

(2) Functional classifications of belowground consumers

Belowground consumers span over twelve orders of magnitude in body mass, inhabit water films and air pores, litter and soil, include all major phyla of terrestrial invertebrates and are highly diverse in feeding habits (Swift, Heal & Anderson, 1979; Scheu, 2002; Coleman, Callaham & Crossley Jr, 2017; Potapov *et al.*, 2021b). To embrace this diversity in forms and functions, consumer species are usually classified into 'guilds' or 'functional groups' that share similar life-history tactics, microhabitats, food, feeding modes and ecophysiology (Brussaard, 1998). In practice, however, classifications focus on different criteria and vary within and among taxa (Briones, 2014; Table 2). For example, nematodes occupy several trophic levels in soil food webs and are classified to 'functional guilds' based on their feeding habits (i.e. plant feeders, bacterivores, fungivores, omnivores, predators and animal parasites) or generation time and response to environmental perturbations (i.e. the coloniser–persister scale) (Bongers, 1990; Yeates *et al.*, 1993; Ferris *et al.*, 2001). These classifications of nematodes allow inferences of stability and energy channelling in soil micro-food webs and evaluation of nutrient enrichment and community disturbance (Ferris *et al.*, 2001).

Taxa with less-clear trophic differentiation, such as springtails, are classified into 'life forms' based on morphology related to their vertical distribution along the soil profile (Gisin, 1943). Subsequently, differences in vertical distribution are associated with differences in ecosystem-level functions: surface-dwelling species alter fungal communities at early stages of litter decomposition, while litter- and soil-dwelling species transform decomposed litter and affect rhizosphere processes (Faber, 1991; Potapov *et al.*, 2016b). Life-form

Table 1. Major groups of consumers that are associated with litter and soil. For supporting references see Section II. ind., individuals

Group	Described species (% associated with soil)	Body length range	Abundance in litter and soil
Protists and microfauna			
Protists	21,000 in soil	0.005–0.05 mm	billions ind. m^{-2} (100–10,000 ind. g^{-1})
Nematoda	50,000 (~50% are associated with litter/soil)	0.1–5 mm	50,000–10,000,000 ind. m^{-2} (1–10 ind. g^{-1})
Rotifera	2100 (~20%)	0.06–2 mm	100–10,000 ind. m^{-2}
Tardigrada	1380 (20–50%)	0.2–1 mm	1000–100,000 ind. m^{-2}
Microarthropods			
Oribatida	10,000 (>95%)	0.2–1.8 mm	2000–300,000 ind. m^{-2}
Astigmata	6000 (<5%)	0.3–1.3 mm	up to 50,000 ind. m^{-2}
Trombidiformes (incl. Prostigmata)	26,000 (30–40%)	0.2–3.5 mm	up to 100,000 ind. m^{-2}
Mesostigmata	12,000 (~50%)	0.3–1.5 mm	up to 50,000 ind. m^{-2}
Pseudoscorpiones	3500 (>90%)	1–8 mm	up to 1000 ind. m^{-2}
Symphyla	201 (>95%)	0.4–10 mm	up to 1800 ind. m^{-2}
Pauropoda	900 (>95%)	0.4–2 mm	up to 2900 ind. m^{-2}
Diplura	1120 (~84%)	1–80 mm	up to 5000 ind. m^{-2}
Protura	800 (>95%)	0.2–2 mm	up to 16,000 ind. m^{-2}
Collembola	9000 (>90%)	0.5–7 mm	3000–100,000 ind. m^{-2} (up to 2,000,000 ind. m^{-2})
Macroarthropods			
Araneae	49,786 (majority partly associated)	0.43–100 mm	131 ind. m^{-2} (worldwide average)
Opiliones	6700 (majority partly associated)	1–10 mm	up to 5 ind. m^{-2} (hundreds*)
Diplopoda	8000 (>90%)	2–300 mm	up to 500 ind. m^{-2}
Chilopoda	3300 (>90%)	5–300 mm	up to 600 ind. m^{-2}
Isopoda	4000 (>90%)	5–30 mm	up to 300 ind. m^{-2}
Dermaptera	1900 (~90%)	7–50 mm	up to 5 ind. m^{-2}
Orthoptera	26,000 (30–40%)	5–150 mm	up to 30 ind. m^{-2} (thousands*)
Embioptera	460 (>90%)	8–25 mm	up to 5 ind. m^{-2}
Blattodea	4640 (>90%)	3–100 mm	up to 50 ind. m^{-2}
Termites	3100 (>80%)	4–15 mm	up to 10,000* ind. m^{-2}
Thysanoptera	6300 (30–50%)	0.5–15 mm	up to 3000* ind. m^{-2}
Hemiptera	100,000 (~50%)	1–110 mm	up to 2000* ind. m^{-2}
Psocoptera	6000 (>75%)	0.6–10 mm	up to 500 ind. m^{-2}
Formicidae	16,000 (>70%)	0.75–20 mm	up to 9000* ind. m^{-2}
Coleoptera	400,000 (>90%)	1–100 mm	300–3000* ind. m^{-2}
Lepidoptera	160,000 (<25%)	1–140 mm	up to 5 ind. m^{-2}
Diptera	160,000 (>75%)	0.4–70 mm	10–5000 ind. m^{-2} (up to >15,000 ind. m^{-2})
Other invertebrates			
Lumbricina	7000 (>90%)	50–150 mm (20 to >1000 mm)	up to 500 ind. m^{-2}
Enchytraeidae	760 (>60%)	1.5–20 mm	up to 100,000 ind. m^{-2}
Gastropoda	25,000 (>95%)	1–200 mm	up to 1000 ind. m^{-2}
Vertebrates			
Amphibia	8403 (70–80%)	1.1–150 cm	up to 2 ind. m^{-2}
Reptilia	11,690 (>70%)	1.4–200 cm	up to 0.2* ind. m^{-2} (2000 ind. ha^{-1})
Aves	10,912 (30–50%)	5.7–275 cm	up to 0.35* ind. m^{-2} (3500 ind. ha^{-1})
Mammalia	6567 (>50%)	3.5–280 cm	up to 0.062* ind. m^{-2} (620 ind. ha^{-1})

*Social/gregarious.

Table 2. Main functional classifications published on soil animals and protists. The table combines related classifications for the same taxonomic group. In part based on Briones (2014)

Consumer group and references	Basis for classification	Categories	References
Protists	Feeding preferences for certain resources or prey.	Phototrophs, algivores, bacterivores, fungivores, saprotrophs, omnivores, predators, plant parasites, animal parasites, microbial parasites	Coûteaux & Darbyshire (1998); Geisen & Bonkowski (2018); Geisen *et al.* (2018a)
Nematodes	Feeding preferences for certain resources or prey.	Plant feeders, bacterivores, fungivores, omnivores, predators, animal parasites	Yeates *et al.* (1993); Bongers & Bongers (1998)
Nematodes	Coloniser–persister (Cp) scale, refers to the *r* and *K* life-history strategies. Reflects generation time and responses to environmental perturbations. High Cp values correspond to high trophic positions.	Cp values from 1 to 5	Bongers (1990); Ferris *et al.* (2001)
Oribatid mites	Feeding preferences for certain resources or other consumers.	Macrophytophages (primary decomposers), microphytophages (secondary decomposers), lichen feeders (including phycophages), panphytophages, zoophages (predators), necrophages, coprophages	Luxton (1972); Maraun *et al.* (2011)
Springtails	Morphological traits related to vertical stratification in the soil profile ('life forms'). Related to feeding preferences for certain resources.	Atmobiotic, epedaphic, hemiedaphic, euedaphic	Gisin (1943); Stebaeva (1970); Faber (1991); Rusek (2007); Potapov *et al.* (2016b)
Earthworms	Morphological traits and vertical stratification in the soil profile. Related to the use of different pools of organic matter.	Three main ecological strategies (epigeic, endogeic, and anecic) with most species occupying intermediate positions	Bouché (1977); Bottinelli *et al.* (2020)
Termites	Feeding preferences for certain resources, gut symbiont community, colony foraging type (simplified in the categories).	Feeding group I (undecayed wood, grass, detritus), II (undecayed wood, fungi, grass, litter, lichens), III (decaying detritus, 'humus'), IV (soil)	Eggleton & Tayasu (2001)

composition of springtail communities further is used to infer their effects on soil functions (Coulibaly *et al.*, 2019), or to indicate environmental changes and soil 'biological quality' (Salmon *et al.*, 2014; Joimel *et al.*, 2017). Similar to springtails, earthworms are traditionally classified into 'ecological groups' based on morphology, vertical distribution in soil and feeding habits (Bouché, 1977; Bottinelli *et al.*, 2020). While epigeic earthworms mostly colonise decaying litter, wood and dung, anecic species live in vertical burrows and translocate litter into the soil, and endogeic species mostly live in the upper mineral soil layers forming horizontal burrows (Bouché, 1977). Ecological categories of earthworms are linked to different pools of organic matter in soil and thus reflect contributions of different species to the carbon cycle (Briones, Garnett & Piearce, 2005; Ferlian *et al.*, 2014; but see Bottinelli & Capowiez, 2021). Classifications based on vertical stratification are also applied to woodlice, gastropods, centipedes, millipedes and other invertebrate groups (Hopkin & Read, 1992; Lewis, 2006; Ellers *et al.*, 2018). All these 'guilds', 'groups', 'forms' and 'categories', despite being developed initially for different purposes, are ultimately applied to indicate the functional roles of consumers in soil as well as to relate community composition to environmental factors.

Overarching functional classifications for soil consumers were described in a number of review papers and monographs on soil ecology (Swift *et al.*, 1979; Lavelle, 1996; Wardle, 2002; Coleman *et al.*, 2017). In these attempts three major functional

Table 3. Basal resources and corresponding trophic guilds of consumers in soil food webs. Synonyms are given in square brackets to align terminology across the text. Main categories are given in Roman font, subcategories in *italics*. Summarised from Swift *et al.* (1979), Striganova (1980), Hunt *et al.* (1987) and Goncharov & Tiunov (2014). Herein, we use the term 'omnivores' for trophic level omnivores, that is consumers feeding on both other consumers (beyond prokaryotes and fungi) and living plant material or detritus; the term 'predators' is used for consumers feeding on other consumers

Basal resource	Description	Consumer trophic guild
Living plant material (P)	Living vascular plant shoots and/or (fine) roots	Herbivores [phytophages]
Detritus (D)	Dead organic matter of plant, microbial or animal origin	Detritivores [animal primary decomposers]
Leaf and root litter (L)	Dead leaves and dead fine roots	Litter grazers [litter transformers]
Wood litter (W)	Dead tree trunks, twigs, branches, large roots, etc.	Wood feeders [xylophages]
Soil organic matter (S)	Residues of microorganisms and other transformed organic matter associated with mineral soil fractions	Soil feeders [humiphages] [geophages]
Animal residues	Dead animals	Necrophages [scavengers]
Microorganisms	Microscopic organisms including prokaryotes, fungi and algae (heterotrophic protists are included in consumers together with animals; phototrophic protists are grouped with algae).	Microbivores [secondary decomposers] [microbiphages]
Prokaryotes [Bacteria] (B)	Free-living heterotrophic prokaryotes, that is most of Bacteria and Archaea.	Bacterivores [bacteriophages]
Fungi (F)	Free-living saprotrophs, mycorrhizal fungi and lichen-associated fungi; predominantly mycelium and spores, but also fruit bodies.	Fungivores [mycophages]
Algae (A)	Phototrophic unicellular organisms including phototrophic protists as well as lichen-associated algae and cyanobacteria.	Algivores [phycophages]

groups are typically distinguished: (*i*) 'micropredators' (protists and nematodes) as microbivores that release nutrients from microbial biomass and directly control microbial populations; (*ii*) 'litter transformers' (mostly detritivorous meso- and macrofauna) that ingest litter and modify its chemical composition and physical structure; and (*iii*) 'ecosystem engineers' (mostly earthworms, termites and ants) that are able to ingest and/or burrow through the soil and thereby modify its structure (Lavelle, 1996). Since the functional and trophic roles of belowground consumers often are defined by their size (Swift *et al.*, 1979; Erktan, Or & Scheu, 2020; Potapov *et al.*, 2021b), the body size spectrum was suggested as an alternative general functional descriptor of soil communities (Mulder, 2006; Turnbull, George & Lindo, 2014). The nematode maturity index, for example, can be considered as a case for the size-spectrum approach since the growth rates and trophic levels of nematodes correlate with their body sizes (Turnbull *et al.*, 2014). Such general approaches, however, are oversimplistic because a 'size class' or a 'litter transformer community' could be assembled out of taxa that differ markedly in feeding preferences and life-history strategies. Thus, the same size spectrum or the same set of broad functional groups may lead to different outcomes in terms of ecosystem functioning (Heemsbergen *et al.*, 2004), and thus to high uncertainty in predictions of the general functional classifications. To build a bridge between the simplicity of the general functional classifications and the complexity of real-world communities, a synthetic approach is needed that links overarching functional roles with group-specific classifications.

(3) Feeding as the functional indicator in soil

Food webs provide a comprehensive framework to link multitrophic biodiversity with ecosystem functioning, because they join functional groups in a single interaction network, and can be used to make inferences on ecosystem functions and stability (Hines *et al.*, 2015; Barnes *et al.*, 2018). As stressed by Brussaard (1998, p.132) "food web models are a starting point from which models should be developed that address non-trophic interactions and the indirect effects of trophic interactions in soil". Roles of consumers in food webs can be primarily defined by their feeding habits, for example consumption of specific resource types, such as leaf litter, roots, bacteria and fungi (Swift *et al.*, 1979; Striganova, 1980; Hunt *et al.*, 1987) (Table 3). Belowground, habitat and food are often the same physical entity (e.g. leaf litter; Fujii, Berg & Cornelissen, 2020) and both litter-transformers and soil feeders modify their environment predominantly by consuming it. Microbial dispersal and community composition is, at least in part, related to feeding activities of microbivores (Vašutová *et al.*, 2019), whereas predators may induce cascading effects on ecosystem functioning by feeding on other consumers (Wardle & Yeates, 1993; Thakur & Geisen, 2019). Such cascading effects can be accounted for by reconstructing predator–prey interactions in food webs (Hunt *et al.*, 1987). Trophic chains based on the same resources are further grouped into 'energy channels', such as bacterial-, fungal- and plant-based channels, forming the core structures of soil food webs (Hunt *et al.*, 1987; de Ruiter *et al.*, 1993). Differentiation between the 'fast' (e.g. bacterial) *versus* 'slow' (e.g. fungal) energy channels and their coupling by top predators has been suggested to drive ecosystem stability (de Ruiter, Neutel & Moore, 1995; Rooney *et al.*, 2006). Thus, soil ecosystem functioning and stability are tightly interlinked with food selection and consumption by individual consumers. Revealing food selection and consumption in soil is, however, not a straightforward task. Direct observations are technically difficult belowground, while laboratory studies often give biased results. In fact, most belowground consumers feed on multiple food resources or prey types (Scheu, 2002; Digel *et al.*, 2014; Wolkovich, 2016). Deeper insights into this 'black box' have been gained recently with advances in molecular, biochemical and isotopic tools (Traugott *et al.*, 2013; Brose & Scheu, 2014; Potapov *et al.*, 2021a), but the emerging knowledge needs to be synthesised across taxonomic groups.

(4) Methods for studying trophic interactions in soil

The question 'Who-eats-whom-and-what?' in soil has been a focus of biologists for many decades (Jacot, 1940). Trophic interactions were traditionally reconstructed from direct observations of feeding behaviour of animals in the laboratory or field, by inspecting gut contents, tracking population changes in consumer–resource systems (Table 4 'Traditional methods') or simply by exploring the morphology of consumers, in particular their mouthparts. Such studies provided the basis for our understanding of feeding habits of belowground consumers and the organisation of soil food webs (Swift *et al.*, 1979; Striganova, 1980). Starting from the 1970s–80s, various new tools were adopted by soil ecologists. These tools are based either on biochemical or molecular assessment of the gut content (i.e. digestive enzymes or prey DNA), or on the analysis of the body tissue composition of the consumer itself (i.e. stable isotopes, radiocarbon, fatty acids and amino acids). The latter approach is based on 'dietary routing', the ability of consumers to incorporate specific molecules unchanged when building their body mass from food (Table 4 'Modern methods'). A number of reviews were published focusing on these methodological approaches (Ruess & Chamberlain, 2010; Traugott *et al.*, 2013; Nielsen *et al.*, 2018; Potapov *et al.*, 2019b; Potapov *et al.*, 2021a) and summarising recent progress in the field of soil food webs (Brose & Scheu, 2014; Bradford, 2016; Geisen *et al.*, 2019). However, a comprehensive understanding of the feeding habits of soil consumers can only be gained by integrating the results of traditional and novel methods and by considering expert knowledge on the biology of consumers. Our review represents a collaborative effort of soil ecologists and taxonomists and aims at achieving such understanding with the following goals: (*i*) review information collected by both traditional and modern tools to describe feeding habits and trophic classifications of belowground consumers, including protists, micro-, meso- and macrofauna and soil-associated vertebrates and to outline their positions in soil food webs. (*ii*) Develop an overarching multifunctional classification based on feeding preferences, body sizes and key functional traits of belowground consumers for soil food-web reconstructions. (*iii*) Evaluate the progress made by novel methods in trophic ecology for different groups of soil consumers and outline promising perspectives for a deeper understanding of their trophic interactions and integration into soil food webs.

II. SYNOPSIS OF FEEDING HABITS

(1) Protists and microfauna

(*a*) *Protists*

Key message: *traditionally considered as bacterivores*, *protists play various roles in soil*, *and also include fungivores*, *predators and parasites of animals and plants*. *Within these groups*, *species-specific preferences exist*. *Further progress in the trophic ecology of protists is expected in particular by using DNA-based tools combined with stable isotope probing*.

Protists are the most abundant and diverse eukaryotes in soils. A single gram of soil commonly contains > 10,000 protists (Stefan *et al.*, 2014), with the number of species being in the hundreds (Geisen *et al.*, 2018a). Also termed protozoa, these heterotroph organisms have been considered among microfauna (Hunt *et al.*, 1987; de Ruiter *et al.*, 1993). Their taxonomy was based on coarse morphological features, dividing them into flagellates, ciliates and amoebae, all of which were considered among the most important predators of bacteria in soils (de Ruiter *et al.*, 1995). Recently, it has been stressed that protozoa are highly intermingled with phototrophic eukaryotes (algae), with many intermediate mixotrophic forms existing and that the morphological groups of flagellates and amoebae are also not monophyletic (Adl *et al.*, 2018). Also, cultivation-independent molecular approaches have revealed that a substantial fraction of protists (sometimes >50% of all sequences) cannot be placed into the classical soil protozoan groups, but that animal parasites, phototrophs and plant pathogens are common in soils (Geisen *et al.*, 2018a). Observational studies and functional experiments have extended the role of protists in food webs from predominantly bacterivores to include fungivores (Ekelund, 1998; Geisen, 2016), predators of larger soil organisms such as nematodes (Geisen *et al.*, 2015b), phototrophs, algivores (Seppey *et al.*, 2017), parasites of soil and aboveground animals (Bates *et al.*, 2013; Geisen *et al.*, 2015a; Mahé *et al.*, 2017), and plant pathogens (Geisen *et al.*, 2015c; Singer *et al.*, 2016). All of these functional groups are present in virtually all soils across the globe (Oliverio *et al.*, 2020).

Even within each of these larger functional units, profound specificity exists; parasites often are highly host specific (Mahé *et al.*, 2017). Bacterivorous protists also select for their preferred prey, which often is determined by bacterial exudates (Schulz-Bohm *et al.*, 2017). Similarly, fungivores and animal predators feed selectively on fungal and nematode species (Geisen *et al.*, 2015b; Geisen, 2016).

Microbivorous free-living protists play an important role in nutrient cycling, releasing nutrients into the soil and

Table 4. Traditional and modern molecular, biochemical and isotopic tools commonly used to study feeding habits of consumers in soil

Method description	Measured parameters	Limitations	Example references
Traditional methods			
Visual observations: feeding behaviour can be directly observed and (qualitatively) described for epigeic species in the field or in the laboratory. Rhizotrons can be used to observe endogeic species	Food preference, Frequency/time of feeding interactions, behavioural traits	Of limited use for cryptic and diverse trophic interactions in soil	Wheeler (1901); Sheppe (1970); Dawson & Byers (2008); Gunn & Cherrett (1993)
Population density experiments: trophic links can be explored using experimental manipulation of consumer (e.g. predator) presence and density in the field or in the laboratory	Magnitude of the population density response	Laborious; trophic and non-trophic effects hard to disentangle	Lawrence & Wise (2000); Schneider & Maraun (2009)
Food choice and reproduction laboratory experiments: attraction of different species to different food resources can be studied with 'cafeteria' multichoice laboratory experiments. Survival and reproduction on specific food resources can be further investigated in no-choice trials	Food preference, survival, reproduction and growth	May not reflect the trophic interactions in complex natural communities	Maraun *et al.* (2003); Scheu & Folger (2004); Bonkowski, Griffiths & Ritz (2000)
Visual gut content analysis: microscopic observations of gut content can inform on the proportion of different basal resources ingested	Proportion of ingested plant material, amorphous detritus, fungi and other particles	In decomposer taxa only a small fraction of the ingested food is assimilated; not suitable for fluid feeders	Bouche & Kretzschmar (1974); Ponge (2000)
Modern methods			
Bulk natural stable isotope analysis: bulk stable isotope composition of carbon and nitrogen in consumer body provides time-integrated quantitative estimate of its feeding on plant *versus* microbial resources and trophic position	Stable isotope ratios (e.g. δ^{13}C and δ^{15}N)	Not suitable for differentiating many basal resources: results can be affected by non-trophic factors at the organism and ecosystem levels	Tiunov (2007); Boecklen *et al.* (2011); Potapov, Tiunov & Scheu (2019b)
Stable isotope labelling: labelling experiments allow tracking of energy and nutrient pathways in food webs over multiple trophic levels by introducing material or organisms that are isotopically distinct from the environment. It can be combined with compound-specific isotope analyses of fatty acids or DNA (stable isotope probing)	Stable isotope enrichment relative to control conditions (e.g. difference in δ^{13}C and δ^{15}N)	Often difficult to design; stable isotope probing is laborious and expensive.	Ostle *et al.* (2007); Crotty *et al.* (2012); Pollierer *et al.* (2012); Kramer *et al.* (2016)
Compound-specific stable isotope analysis of amino acids: can distinguish between different	Stable isotope ratios (e.g. δ^{13}C and δ^{15}N) in individual amino acids	Laborious and not suitable for microfauna; gut microbial contributions (^{13}C) and	Pollierer et al. (2019); Pollierer, Scheu & Tiunov (2020)

(Continues)

Table 4. *(Cont.)*

Method description	Measured parameters	Limitations	Example references
types of microorganisms in the diet and estimate trophic positions of consumers precisely in a time-integrated and quantitative way		variation in trophic fractionation among consumer types (^{15}N) can hamper interpretation	
Fatty acid profiles: fatty acid biomarkers allow tracing of the channelling of basal food resources such as plant material, fungi and bacteria, in consumers across trophic levels. This method does not allow estimation of trophic position but distinguishes feeding on several groups of basal resources (e.g. fungi, bacteria, plants, algae).	Concentrations or relative proportions of biomarker fatty acids (NLFAs)	Laborious and technically not suitable for microfauna; semi-quantitative	Pollierer, Scheu & Haubert (2010); Ruess & Chamberlain (2010); Kühn *et al.* (2020)
Molecular gut content analysis (diagnostic polymerase chain reaction): taxon-specific target gene amplification in the gut (or the whole body) can provide detailed information about ingestion of certain groups or species of other organisms by the consumer	Detection (yes/no) of a specific prey group or a species	Provides cost-efficient diet snapshot from a single time point for a single prey type; semi-quantitative (frequency analysis); primer specificity is hard to quantify	Heidemann *et al.* (2011); Eitzinger *et al.* (2013)
Molecular gut content analysis (Next-generation sequencing): metabarcoding of a target gene in the consumer gut (or the whole body) can provide information on the ingestion of other organisms by the consumer (down to the species level)	Relative abundances of different DNA-based species in the diet	Provides diet snapshot from a single time point; semi-quantitative (amplification bias is hard to omit, host DNA is predominantly amplified)	Eitzinger *et al.* (2019); Gong *et al.* (2018); Rennstam Rubbmark *et al.* (2019); Hao *et al.* (2020)
Digestive enzyme analysis: activity of different digestive enzymes in the consumer body (i.e. gut), such as cellulase, chitinase and trehalase. The method suggests the ability of consumers to digest specific substrates and reflects potential assimilation of different basal resources and feeding strategies (such as grazing on poor-quality food *versus* browsing for palatable food).	Presence/absence and activity (reaction rate) of specific enzymes	Laborious and not suitable for microfauna; provides evidence only on potential food assimilation	Siepel & de Ruiter-Dukman (1993); Berg, Stoffer & van den Heuvel (2004)

making them available for plant uptake and growth, thereby catalysing the microbial loop in soil and modifying plant performance (Bonkowski, 2004). Especially free-living protist predators serve as prey for higher trophic levels in food webs, for example predatory nematodes (de Ruiter *et al.*, 1995). However, this single link likely underestimates the function of protists in soil, as stable isotope analyses revealed that various groups of soil animals also take up protist-derived nutrients (Crotty *et al.*, 2012).

High-throughput sequencing tools recently showed that community composition of protists is often tightly linked within soil microbial communities, particularly with bacteria (Xiong *et al.*, 2018; Wilschut *et al.*, 2019b), adding support to the role of protists as a main structural element for bacterial communities. This corroborates stable isotope data on the trophic position of slime moulds (Myxomycetes) (Tiunov *et al.*, 2015). Yet, links between predator–prey communities can differ among soils (Zhao *et al.*, 2019) rendering general conclusions about the relative role of bottom-up or top-down forces as well as which microbial groups most strongly determine protist communities impossible. Also sequence-based stable-isotope probing (DNA/RNA SIP) has been used to show assimilation of root-derived nutrients by soil protists likely through predation on other microorganisms (Kramer *et al.*, 2016; Hünninghaus *et al.*, 2019).

Unfortunately, many methods used to study soil organisms cannot be applied to protists as their highly paraphyletic nature always identifies them as animals in general marker-analyses such as that of phospholipid fatty acids, while cultivation approaches select for a tiny fraction of protists (Geisen & Bonkowski, 2018). Furthermore, protists are single-celled and their biomass is too small for most techniques. As such, the method of choice currently is molecular (mostly sequence-based) analyses of complex protist communities in soils that can be combined with isotopic labelling, while feeding preferences allow specific insights into food preferences of individual taxa (Geisen & Bonkowski, 2018). This will likely change the perception of protists functioning mainly as bacterial feeders and help to unravel the exact position of distinct protist groups in the soil food web.

(*b*) *Nematoda*

Key message: based on mouthpart morphology nematodes are classified into plant feeders, bacterivores, fungivores, omnivores, predators and animal parasites. Novel methodologies generally support this classification. High-rank taxonomy or DNA identification can be used to assign nematodes to different feeding guilds.

The most abundant animals in soils and on Earth in general are nematodes (van den Hoogen *et al.*, 2019). Their abundance reaches millions per square meter in temperate grassland ecosystems (Sohlenius, 1980). This group of microscopic invertebrates is considered as microfauna and with over 25,000 soil-associated species described has a long tradition in soil studies (Geisen *et al.*, 2019). This has made nematodes one of the best-known groups of soil taxa leading to the establishment of a number of soil quality indices based on nematode analyses (Bongers, 1990, 1999; Ferris *et al.*, 2001; Ferris & Bongers, 2006). This is also true for food-web analyses in which nematodes arguably are best known and represented; one of the reasons being that nematodes can be easily assigned to feeding groups based on their mouthparts; with these groups including bacterivores, fungivores, plant feeders, omnivores, predators and animal parasites (Yeates *et al.*, 1993).

Each of these feeding groups is of key importance. Bacterivorous, fungivorous, omnivorous and predatory nematodes form central hubs in soil micro-food webs (de Ruiter *et al.*, 1995). Plant-feeding nematodes presumably are the most important root herbivores, causing massive economic damage in arable systems (Neher, 2010) and controlling the succession of plant communities in natural ecosystems (Van der Putten, Van Dijk & Peters, 1993; Wilschut *et al.*, 2019a). Although interactions with other soil organisms have been studied intensively, for example with nematode-trapping fungi, to explore their biocontrol potential, it remains difficult to control root-feeding nematodes, presumably due to the complexity of soil food webs and the lack or rarity of species-specific links. Although usually ignored in food-web studies, entomopathogenic nematodes also are important components of soil food webs that kill larger animals, particularly insect larvae, and thereby reduce damage to roots by root-feeding insect larvae (Lacey & Georgis, 2012).

Feeding preferences of nematodes can vary within feeding groups. For instance, root-feeders selectively feed on certain plant species and this results in important feedbacks to nematode community composition (Wilschut *et al.*, 2019b). Also bacterivorous nematodes and fungivorous nematodes have been shown to select certain prey taxa in laboratory experiments (Dighton, Zapata & Ruess, 2000; Liu *et al.*, 2017). Feeding on organisms outside the actual feeding group is common, such as some root-feeding nematodes that also prey on fungi (Okada, Harada & Kadota, 2005) and even prefer non-plant food sources such as algae and fungi (Newsham *et al.*, 2004). Some larger predators start their life as bacterivores when they are juveniles (Yeates *et al.*, 1993).

Nematodes themselves are prey to larger, predacious or omnivorous nematodes, but also to diverse nematophagous and predatory mites and springtails (de Ruiter *et al.*, 1995; Heidemann *et al.*, 2014a). While profoundly explored for applied purposes, the importance of nematophagous fungi and other taxa that prey on nematodes in natural ecosystems remains little investigated. Overall, however, the key importance of nematodes in soil food webs is illustrated by their positioning across several trophic levels and functional groups (Ferris, 2010; Ferris *et al.*, 2012).

Profound knowledge on feeding preferences of nematode taxa was gained by laboratory feeding experiments, which allowed placing nematodes into feeding groups (Yeates *et al.*, 1993). Using stable isotope analysis for individual nematode taxa in general confirmed the morphology-based feeding groups (Kudrin, Tsurikov & Tiunov, 2015; Melody *et al.*, 2016; Shaw *et al.*, 2018). Further, fluorescent *in situ* hybridisation (FISH) provided high-resolution prey-detection in individual nematodes (Treonis *et al.*, 2010); alternatively, specifically sequencing nematode guts can inform both about potential prey but also microbial gut symbionts (Berg *et al.*, 2016). Fatty acid profiles were suggested as a cost-efficient method to track changes in trophic niches of nematode communities in different environments (Kühn *et al.*, 2018). Molecular techniques used to study nematode communities (quantitative polymerase-chain reaction, high-throughput sequencing) are combined with taxonomy-based classifications (Geisen *et al.*, 2018b; Schenk *et al.*, 2019), or correlated with potential prey (Wilschut *et al.*, 2019a) to infer taxon-specific food relationships. Taken together, these approaches have helped to showcase specificity within nematode feeding groups and provided various tools for a rapid assessment of soil micro-food webs.

(*c*) *Rotifera*

Key message: *soil rotifers live as filter feeders*, *predominantly on bacteria*. *However*, *some taxa also feed on other metazoans*, *algae or biofilms*.

Rotifers are filter-feeding microfauna living predominantly in fresh water with around 400 species known from soil, litter, mosses and lichens (Kutikova, 2003). They are abundant in most ecosystems, but often are overlooked because of their small size, no evident impact on ecosystem processes and difficult determination. Rotifers preferentially colonise the upper litter layer, but some species are more abundant in soil (Devetter, 2009b). Around 90% of soil rotifer species belong to Bdelloidea and about 10% to Monogononta (Varga, 1959; Donner, 1972). Bdelloidea with the ramate type of trophi (a solid structure in the anterior part of the digestive tract) are microphagous filter-feeders exploiting bacteria (*sensu lato*), detritus and algae (Dunger, 1964; Pourriot, 1979). This information, however, is based on few early microscopic observations (Donner, 1972). Experimental studies on trophic links of soil rotifers are scarce (Coleman & Crossley Jr, 1995), and virtually all data on the food and feeding of bdelloid rotifers originate from fresh water.

Rotifers use cilia for filtering small particles suspended in water and passing them to the mouth (Pourriot, 1979). This unique feeding mode in soil resembles that of flagellates and ciliates. Using fluorescent particles of bacterial size, Devetter (2009b) estimated *Habrotrocha thienemanni* individuals to clear 40–90 μl of water per day. Rotifers are able efficiently to filter particles as small as 0.3 μm in diameter (Devetter, 2009a), thereby being able to feed on a wide range of bacteria. However, bdelloid rotifers may feed selectively on certain bacteria (Wallace & Starkweather, 1983). Some species, such as *H. thienemanni*, were suggested to be exclusively bacteriophagous (Dougherty & Solberg, 1959; Pourriot, 1979), whereas other bdelloid species preferentially feed on green algae and cyanobacteria in biofilms (Pourriot, 1979; Mialet *et al.*, 2013), consuming up to 8–9 times their body mass of algae per day (Erman, 1956). By contrast, the reduced corona of members of the family Adinetidae (including the common soil genus *Adineta*) and species of the genera *Wierzejskiella* and *Bryceella* (Monogononta) crawl on surfaces and scrape biofilms with cuticular rakes or cilia (Melone & Ricci, 1995). Predators of other eukaryotes are represented by the genus *Encentrum* (Monogononta) and by the species *Abrochtha carnivora* (Bdelloidea; Ricci, Melone & Walsh, 2001). Among novel methods, stable isotope analysis has been used recently to compare the trophic position of rotifers and tardigrades, suggesting a higher trophic position for rotifers (Novotná Jaroměřská *et al.*, 2021).

Overall, three trophic groups of rotifers may be recognised in soil: microbial (bacterial) filter feeders (most bdelloid species), microbial scrapers (Adinetidae, *Wierzejskiella*) and carnivores (*Encentrum* and *Abrochtha carnivora*). The general importance of rotifers in soil food webs, their degree of algivory and selective feeding on bacteria species need to be clarified in future studies.

(*d*) *Tardigrada*

Key message: *tardigrades feed as herbi-fungi-bacterivores, but larger species also as omnivores and carnivores by piercing their prey with the stylets. Generalist feeding is likely to occur in all groups.*

Tardigrades are micrometazoans comprising 1380 species from marine, freshwater and terrestrial environments (Degma, Bertolani & Guidetti, 2021). They depend on the presence of water for activity but can survive drought in cryptobiosis and reach high abundances in soils that periodically dry out (Nelson, Guidetti & Rebecchi, 2015). Their significance for ecosystem processes presumably is more profound in systems where meso- and macrofauna are scarce, for example in polar regions and in disturbed habitats (Hyvönen & Persson, 1996; Sánchez-Moreno, Ferris & Guil, 2008).

The diet of tardigrades includes bacteria, detritus, fungi, algae, mosses, protists and micrometazoans such as nematodes, rotifers and other tardigrades, while they may fall prey to nematodes, other tardigrades, oligochaetes, springtails, mites, spiders and insect larvae (Nelson *et al.*, 2015). Feeding on algae and microfauna is well described from cultures (Altiero & Rebecchi, 2001; Hohberg & Traunspurger, 2005). However, feeding on other types of food is poorly documented. Bacteria and detritus were mentioned as possible food of tardigrades, but their role in tardigrade nutrition has never been evaluated experimentally (Hallas & Yeates, 1972; Hohberg & Traunspurger, 2005; Hohberg, 2006). Fungi have been confirmed recently as food for tardigrades in a manipulative experiment (Bryndová *et al.*, 2020). Feeding on mosses was confirmed by PCR in Macrobiotidae, and the presence of carotenoids of moss origin in Echiniscidae has been revealed by *in-vivo* chemical analysis using Raman micro-spectroscopy (Schill *et al.*, 2011; Bonifacio *et al.*, 2012). Stable isotope analysis suggested that tardigrades inhabiting the surface of glaciers may occupy a lower trophic position than rotifers (Novotná Jaroměřská *et al.*, 2021). Herbivores, omnivores, carnivores and occasionally microbivores have been recognised in ecological studies on tardigrades (Hallas & Yeates, 1972; Guil & Sanchez-Moreno, 2013; Vonnahme *et al.*, 2016; Buda *et al.*, 2018; Zawierucha *et al.*, 2019). However, trophic guilds are poorly defined. There is a lack of experiments that inspect the differences in the diets of anatomically different feeding groups. Moreover, microbivores as well as carnivores have been observed to feed on algae (M. Bryndová, personal observations; Tumanov, 2006). Feeding generalism thus might be more widespread than anticipated (Bryndová *et al.*, 2020). The anatomy of the feeding apparatus and current knowledge on the tardigrade diet suggests that tardigrades can be divided into two feeding groups. The first group, herbi-fungi-bacterivores, have generally small body size and feeding apparatus, and the second group, omnivores and carnivores, have generally large body size and feeding apparatus (Guidetti *et al.*, 2012). The genus *Hypsibius* represents a typical herbi-fungi-bacterivore tardigrade with a narrow buccal tube, subtle stylets and small pharynx. By contrast, the genus *Paramacrobiotus* represents a typical omnivore of large body size, wide buccal tube, robust stylets and large pharynx (Guidetti *et al.*, 2012). For a more detailed classification of tardigrades into trophic guilds, links between anatomy and diet need to be studied more intensively. With further technical improvements, modern methods (e.g. stable isotope analysis; Novotná *et al.*, 2021) should be applied to microfauna and to investigate tardigrade feeding preferences in anatomically different feeding groups.

(2) Microarthropods

(*a*) *Oribatida*

Key message: oribatid mites are not a single trophic group but belong to four or more trophic guilds as indicated by stable isotope (^{15}N, ^{13}C) analyses including lichen feeders, primary decomposers, secondary decomposers and predators/scavengers. Classification into the trophic guilds above the species or genus level is not reliable in most cases.

Oribatid mites are diverse and abundant mesofauna in nearly all terrestrial ecosystems (Maraun & Scheu, 2000; Maraun, Schatz & Scheu, 2007). Their densities range from a few thousand individuals per square meter in arid, agricultural and tropical soils to more than 200,000 individuals per square meter in acidic temperate or boreal forests (Maraun & Scheu, 2000). With about 10,000 described species, their worldwide species diversity is moderate (Subías, 2004; Schatz & Behan-Pelletier, 2008), but their local alpha diversity is typically high (Giller, 1996; Lindo & Winchester, 2008). A mechanism that may contribute to their coexistence is trophic specialisation on certain food types (e.g. certain species of soil fungi). However, evidence for specialised feeding of soil-living oribatid mites on a narrow spectrum of fungi or other food resources is rare or lacking entirely. In fact, considering that the mobility of animals in the soil matrix is restricted, resulting in high search time, the evolution of trophic specialisation appears to be unlikely.

Considering their high abundance, one may expect Oribatida to represent important prey for soil-dwelling predators. However, as stressed repeatedly, Oribatida are very well protected against predators by a variety of morphological and biochemical mechanisms (Norton & Behan-Pelletier, 1991; Raspotnig *et al.*, 2001; Sanders & Norton, 2004; Heethoff *et al.*, 2011). Indeed, well-sclerotised adults have been shown to be protected against generalist predators in soil such as mesostigmatic mites (Peschel *et al.*, 2006; Brückner *et al.*, 2016). However, juveniles, which are much less protected by sclerotisation, may well be preyed upon by a wide range of predators including generalists, such as mesostigmatic mites and centipedes. Some specialists, such as Ptiliidae and Pselaphidae beetles, may also feed on adults of oribatid mites. Unfortunately, evidence from the field on the relative importance of Oribatida as prey in soil food webs is virtually entirely lacking. Novel methods including molecular gut content analysis may help to clarify this issue. Although group-specific primers allowing screening for Oribatida as prey in soil food webs have been developed (Eitzinger *et al.*, 2013), they have not yet been used in the field.

The role of oribatid mites in ecosystem processes is little understood, in part due to limited information about their trophic ecology. Different species may feed on freshly fallen litter material, fungi, decomposing organic material, bacteria, lichens, algae, mosses or may even act as predators or scavengers (Forsslund, 1938; Riha, 1951; Harding & Stuttart, 1974; Anderson, 1975; Lions & Gourbière, 1988; Maraun *et al.*, 2011). In many ecological studies, oribatid mites have been lumped into a single trophic group (Haimi, Fritze & Moilanen, 2000; Wardle *et al.*, 2006; Moore & de Ruiter, 2012); such grouping is clearly inadequate, given the progress that has been made in understanding the trophic ecology of Oribatida, especially in recent decades.

Feeding experiments showed that oribatid mites consume a wide range of fungi (Hartenstein, 1962; Luxton, 1966; Martin, 1979) with preferences for dark-pigmented rather than hyaline fungal taxa (Mitchell, 1976; Schneider & Maraun, 2005) and for non-mycorrhizal rather than mycorrhizal fungi (Schneider *et al.*, 2005). However, microcosm experiments showed that at least *Oppiella nova* benefits from the presence of mycorrhizal fungi (Remén *et al.*, 2010).

Early laboratory studies resulted in the aggregation of oribatid mite species into three functional groups (Schuster, 1956; Wallwork, 1958; Luxton, 1972). Macrophytophagous taxa were assumed to feed on decomposing plant material, microphytophagous taxa included species that consume algae, fungi and bacteria, and more generalist feeders, combining both plant material and microbes in their diet, were classified as panphytophagous. Starting in the 1970s, enzyme activities in oribatid mites, including for example cellulase, chitinase and trehalase, were used for grouping oribatid taxa into trophic groups (Zinkler, 1971; Luxton, 1972, 1979; Siepel & de Ruiter-Dukman, 1993). Siepel & de Ruiter-Dukman (1993) distinguished five major trophic guilds based on the combination of enzymatic activities: herbivorous grazers, fungivorous grazers, herbo-fungivorous grazers, fungivorous browsers and opportunistic herbo-fungivores.

The abovementioned studies have been summarised in Schneider *et al.* (2004), who also introduced stable isotope analysis as a novel tool for investigating trophic niches of oribatid mites. Using $\delta^{15}N$ values as an indicator for trophic position, it became evident that oribatid mites occupy 3–4 different trophic levels (Schneider *et al.*, 2004). The study documented at least four trophic groups, that is (*i*) phycophages, presumably feeding predominantly on lichens and algae, (*ii*) primary decomposers, mainly feeding on dead organic material poorly colonised by microorganisms, (*iii*) secondary decomposers, mainly feeding on microorganisms and microbial residues, and (*iv*) predators and/or scavengers. Based on the combination of $\delta^{15}N$ and $\delta^{13}C$ values, moss-dwelling oribatid mite species of the genera *Melanozetes* and *Edwardzetes*, have been concluded to feed on mosses (Fischer, Schatz & Maraun, 2010; Bluhm, Scheu &

Maraun, 2015). Stable isotope analysis, however, needs to be interpreted with care, since some oribatid mites, such as Phthiracaridae, incorporate calcium carbonate in their cuticle (Norton & Behan-Pelletier, 1991) and thus have very high δ^{13}C values. Overall, stable isotope studies point to strong trophic niche differentiation among species, with niches for a given species being similar across ecosystems under moderate environmental changes (but see Krause *et al.*, 2019).

Neutral lipid fatty acid (NLFA) analysis has been proved to reflect well the food resources used by oribatid mites (Brückner, Hilpert & Heethoff, 2017), but field studies are rare. NLFA patterns confirmed trophic niche differentiation among oribatid mite species in temperate forests, and that niches of the entire community overall differ between spruce and beech forests (Maraun *et al.*, 2020). Widespread occurrence of bacterial NLFA biomarkers in different species further suggests that bacteria may be underestimated as a food source for oribatid mites (Maraun *et al.*, 2020). However, using compound-specific amino acid analysis, Pollierer & Scheu (2021) recently found oribatid mites of temperate forests to feed predominantly on saprotrophic fungi rather than bacteria.

Molecular (DNA) gut content analysis showed that oribatid mites frequently consume nematodes in the laboratory and in forest habitats, indicating that this trophic link has been underestimated in the past (Heidemann *et al.*, 2011, 2014a,b). Using specific DNA primers, nematode prey has been detected in a wide range of oribatid mite taxa that have previously been assumed to live as primary or secondary decomposers, such as *Platynothrus* and *Nothrus*, and also in species that were earlier assumed to be predators or scavengers, including Belbidae, Galumnidae, *Nothrus* spp., Oppiidae, Scheloribatidae, Suctobelbidae and *Tectocepheus* (Riha, 1951; Rockett & Woodring, 1966; Muraoka & Ishibashi, 1976; Rockett, 1980; Maraun *et al.*, 2011).

In sum, considerable progress has been made in understanding the trophic ecology of oribatid mites and their position in soil food webs in recent decades. The term "choosy generalists" used for oribatid mites by Schneider & Maraun (2005) summarises the conundrum that on one hand oribatid mites appear to be trophic generalists, but on the other hand occupy distinct trophic niches as indicated by stable isotope and lipid analyses. Oribatid mite species belong to at least four trophic guilds, and the trophic niche of many species is rather predictable across ecosystems. Some systematic differences in trophic position were recorded also for oribatid mite families across temperate and tropical ecosystems (Tsurikov, Ermilov & Tiunov, 2020), but overall there is a poor connection between trophic position and phylogenetic relationships of oribatid mites, suggesting frequent convergent evolution of similar trophic positions across taxa (Schaefer & Caruso, 2019). This significantly complicates the assignment of species to guilds based on high-rank taxa.

Future studies should focus on the following topics: (*i*) the importance of bacterial *versus* fungal feeding may be explored further using quantitative fatty acid and compound-specific amino acid analysis (Kühn, Schweitzer & Ruess, 2019; Pollierer & Scheu, 2021); (*ii*) understanding species-specific interactions with fungi as well as prey species can be achieved using molecular gut content analysis; (*iii*) understanding coevolutionary processes of gut microorganisms with their host, and their contribution to digestion processes, which can be uncovered by metabarcoding of the gut microbiome (Gong *et al.*, 2018); (*iv*) trophic flexibility of oribatid mite species with specific habitat and food requirements, such as microorganisms associated with dead wood (Bluhm *et al.*, 2015) or agricultural sites (Krause *et al.*, 2019) which can be assessed using stable isotope analyses (^{15}N; ^{13}C).

(*b*) *Astigmata*

Key message: the few known soil-dwelling astigmatic mites can be classified as microbivores-detritivores, feeding on fungi, algae and detritus, or as omnivores when opportunistically feeding on microfauna or plant tissues.

Astigmata is a diverse lineage of over 6,000 known species of parasitic, commensal and free-living mites that originated within the Oribatida (OConnor, 2009; Schatz *et al.*, 2011). In contrast to Oribatida (*sensu stricto*), free-living astigmatic mites are specialists of patchy habitats such as dead wood, animal nests, dung and compost, which they colonise using phoresy on insects. They are generally soft-bodied, move slowly, and build up populations rapidly. Relatively few genera of Astigmata (e.g. Acaridae: *Tyrophagus*, *Sancassania*, *Schwiebea*) occur in soil habitats (Philips, 1990). Although these taxa are usually primarily deemed fungivores or microbivores, they will frequently supplement their diet with other microinvertebrates such as nematodes, protozoans and rotifers, or scavenge on dead invertebrates or rotting plant material (Walter & Kaplan, 1990; Walter & Proctor, 2013). Species of *Tyrophagus* have been reared on fungi, but also on nematodes alone, clearly showing the potential of these mites to act as predators (Walter, Hudgens & Freckman, 1986). A few species can feed directly on plant tissues, especially when the plant has been damaged and/or previously weakened by fungi on which they also feed, such as *Acarus* on seeds and *Rhizoglyphus* on bulbs and tubers (Sinha, 1979; Díaz *et al.*, 2000). Like Oribatida, they are particle-feeders, biting off pieces of detritus and fungi and swallowing them (OConnor, 2009; Walter & Proctor, 2013). Among astigmatic mites, histiostomatids are exceptional in their feeding style as they filter-feed on microbes from moist surfaces including wet litter and other pockets of rotting organic matter (Walter & Kaplan, 1990). Soil-dwelling Astigmata are preyed upon by other small arthropods such as mesostigmatic and prostigmatic mites and other predators such as symphylans (Walter, Hunt & Elliott, 1987; Walter, Moore & Loring, 1989; Crotty & Adl, 2019). The few available data based on stable isotopes suggest that soil-dwelling Astigmata occupy similar trophic positions to Oribatida, thus being detritivores, microbivores or omnivores, depending on the food available (Bücking, 1998; Crotty *et al.*, 2014).

(*c*) *Trombidiformes (including Prostigmata)*

Key message: soil-dwelling trombidiform mites occupy all major feeding guilds, including predators, fungivores-microbivores, plant feeders and parasites, some of which also act as omnivores. Substantial research is needed on this poorly explored mite group for elucidating food resources used by taxa.

Trombidiformes, represented primarily by Prostigmata, is a diverse mite lineage of about 26,000 known species, with many more undescribed (Zhang *et al.*, 2011). Their microhabitats are extremely varied and a large number of taxa inhabit soil and litter of all terrestrial biomes including deserts. Their feeding habits differ widely among – even sometimes related – families, genera and species (Kethley, 1990; Walter *et al.*, 2009; Coleman *et al.*, 2017). For some families, food resources are entirely unknown. Like Mesostigmata, Trombidiformes are essentially fluid-feeders, sucking the contents of animal, plant or fungal substrates, and the evolution of these piercing–sucking mouthparts certainly facilitated the diversification of their feeding habits among and within families (Lindquist, 1986). Although some species of soil-dwelling Prostigmata are specialised for certain types of food, many are more opportunists. For instance, among the known (and many more suspected) fungivorous Prostigmata, some are also facultative predators of nematodes (e.g. Eupodidae, Tydeoidea) (Walter, 1988). Some fungivores may also feed on lichen or unicellular algae (Walter *et al.*, 2009). Some genera (of Stigmaeidae and Eupodoidea) are known or suspected to feed on mosses at some point in their life cycle (Gerson, 1972; Walter & Proctor, 2013). This apparent omnivory varies in breadth among species and probably also among life stages, locations and seasons, and is yet to be determined for the majority of species of Prostigmata.

Several families appear more homogeneous in their feeding style, with all constituent species considered as predators (Kethley, 1990). Like predatory Mesostigmata, Prostigmata are often deemed generalist predators, but species have major preferences for certain prey types, such as nematodes, soft-bodied arthropods, or even their eggs. Preferred prey may be related to their size or behaviour. For instance, some Prostigmata are ambush predators (e.g. some Bdellidae, Cunaxidae, Cheyletidae) and will only attack active prey such as springtails and other mites, whereas cruise predators will tend also to include slow or sessile prey such as nematodes or invertebrate eggs in their diet. Intraguild predation is also common, as well as cannibalism, at least in the absence of other food sources (Walter, Hunt & Elliott, 1988; Walter & Kaplan, 1991; Gerson, Smiley & Ochoa, 2003).

Many Prostigmata encountered in soil–litter are ectoparasites of insects and other animals including vertebrates. The clade Parasitengona adds another layer of complexity because the larvae of most species are parasites whereas postlarval stages are predators of invertebrates, especially in the soil. Some of them complement their diet with pollen, expanding their trophic breadth to omnivory. As for other groups of mites (Mesostigmata, Astigmata), some Prostigmata are associated with animals (e.g. beetles, bees, mammals, reptiles) that nest in the ground or nearby substrates such as dead wood (Eickwort, 1994; Haas *et al.*, 2019). The mites' feeding activity as saprophages, pollen feeders, parasites or predators in the nests may be further reinforcing connections of trophic channels from aboveground to belowground webs. Similarly, many species wander from soil–litter habitats to aboveground plant parts, feeding on various food sources including plant-feeding mites and insects (Walter & Proctor, 2013).

Some members of strictly phytophagous families (e.g. Linotetranidae, Tuckerellidae) or genera (*Steneotarsonemus*) are suspected to feed on the roots of grasses, and species of Penthaleidae are common in litter and feed on low-growing plants, at least as adults (Beaulieu & Knee, 2014). Other phytophagous mites (e.g. Tetranychidae) otherwise inhabiting plant foliage use litter as a temporary refuge, especially during winter, and may be preyed upon by soil-dwelling predators. In contrast to the heavily sclerotised Oribatida and most Mesostigmata, Prostigmata tend to have a thin cuticle and thus lower protection from predators like other mites and larger arthropods such as spiders (Walter *et al.*, 1987; Walter & Proctor, 2013). The few existing data on stable isotopes suggest that soil-dwelling Trombidiformes overall occupy an intermediate trophic position between Oribatida and Mesostigmata (Crotty *et al.*, 2014). Addtional data are badly needed from available methods (Table 4) to shed more light on the food resources used by individual species, as well as on microhabitat preferences, including for species using both below- and aboveground substrates and those with ecology shifting during ontogeny. Community studies should preferably be based on species-level or at the very least family-level identifications to permit sorting into coarse trophic guilds.

(*d*) *Mesostigmata*

Key message: soil-living mesostigmatic mites are primarily predators of micro- and mesofauna, coupling root-, detritus- and microbial-based energy channels. Nematodes and soft-bodied microarthropods are their main prey. Mesostigmata tend to occupy high trophic positions in soil food webs, functioning as generalist and intraguild predators.

Mesostigmatic mites (Mesostigmata) are taxonomically diverse with over 12,000 known species and are especially abundant and species-rich in forest, grassland and agricultural soils (Koehler, 1999; Beaulieu & Weeks, 2007; Kaspari & Yanoviak, 2009; Beaulieu *et al.*, 2010; Young, Behan-Pelletier & Hebert, 2012; Walter & Proctor, 2013; Seniczak *et al.*, 2018). Although microhabitat and feeding preferences of Mesostigmata are diverse – encompassing vertebrate parasites, arthropod symbionts, fungivores and pollenivores in specialised habitats – the majority of species are free-living predators in soil-litter habitats (Krantz & Ainscough, 1990; Karg, 1993; Beaulieu & Weeks, 2007; Lindquist, Krantz & Walter, 2009). Fungivory and scavenging have been documented in soil-dwelling species, but these feeding strategies are mostly regarded as opportunistic or facultative (Karg, 1989; Walter & Lindquist, 1989; Walter & Proctor, 1998; Beaulieu & Walter, 2007). The capacity to feed and even reproduce on fungi appears limited to a few genera (e.g. of Ameroseiidae) or species within genera (e.g. Ascidae, Blattisociidae, Digamasellidae). Laboratory experiments suggest that predatory Mesostigmata either feed preferentially on prey of relatively low mobility (e.g. nematodes, enchytraeids, insect larvae, arthropod eggs), on soft-bodied microarthropods (e.g. Collembola, weakly sclerotised mites), or are generalists, having the ability to utilise various types of prey (Walter *et al*., 1988; Karg, 1989, 1993; Beaulieu & Walter, 2007). However, prey spectra of Mesostigmata overall seem to include most prey they can seize. For instance, nematodes are accepted as prey by most species when encountered (Walter *et al*., 1988; Walter & Ikonen, 1989; Beaulieu & Walter, 2007). Reflecting this, classic food-web models include Mesostigmata in broadly defined and non-mutually exclusive categories such as "predaceous mites" and "nematophagous mites" (Hunt *et al*., 1987; De Ruiter *et al*., 1993). With few exceptions, the structure of Mesostigmata mouthparts and alimentary tracts restricts this group to liquified food (Walter & Proctor, 1998). Accordingly, microscopic gut content analyses provide little insight into the composition of their diets. Nevertheless, the feeding state of field-caught individuals may be assessed visually by observing states of the midgut (Bowman, 2017).

Investigations of natural stable isotope ratios allow conclusions about the diets of Mesostigmata in the field and complement information gained from laboratory feeding trials. Nitrogen stable isotope signatures indicate that non-predatory feeding is of minor importance and that all species investigated occupy high trophic positions (Díaz-Aguilar & Quideau, 2013; Klarner, Maraun & Scheu, 2013; Haynert *et al*., 2017; Lagerlöf, Maribie & Muturi, 2017). This essentially predatory lifestyle also extends to many species of Uropodina, a taxonomic group otherwise comprising at least some fungivores–microbivores (Lindquist *et al*., 2009). Hypotheses on the trophic structure of soil animal communities that integrated Uropodina as a fungivorous group (Persson *et al*., 1980; Axelson, Lohm & Persson, 1984; Hunt *et al*., 1987) should therefore, at least in part, be reconsidered. Nitrogen stable isotope signatures of several Mesostigmata species were found to vary considerably, indicating that their prey originate from different trophic levels and potentially include primary decomposers, secondary decomposers and other predators (Díaz-Aguilar & Quideau, 2013; Klarner *et al*., 2013; Crotty *et al*., 2014; Haynert *et al*., 2017; Lagerlöf *et al*., 2017); secondary decomposers (microbivores) likely constitute the main prey, but intraguild predation may also be significant (Klarner *et al*., 2013; Crotty *et al*., 2014; Haynert *et al*., 2017). Combined data on carbon and nitrogen stable isotope ratios indicate trophic niche separation between closely related species (Klarner *et al*., 2013; Haynert *et al*., 2017).

Isotopic labelling approaches also emphasise trophic links between microbivores and Mesostigmata. The ability to feed on bacterivorous nematodes provides many species with access to root-derived resources (Ruf, Kuzyakov & Lopatovskaya, 2006; Lemanski & Scheu, 2014), whereas feeding on other prey groups, such as fungivorous Collembola, enable accessing fungal-based nutrients (Crotty & Adl, 2019).

Consumption of bacterivorous nematodes was successfully traced under field conditions using molecular (PCR-based) methods in species sampled from temperate forest litter (Heidemann *et al*., 2014a,b). PCR-based approaches were also employed for investigating Mesostigmata as part of diets of other predators such as centipedes and wolf spiders in temperate forests and the Arctic, respectively (Eitzinger *et al*., 2018, 2019).

The trophic positions of Mesostigmata species do not appear to be significantly correlated with body size (Díaz-Aguilar & Quideau, 2013; Klarner *et al*., 2013; Lagerlöf *et al*., 2017). Correlations between more complex morphological features, such as cheliceral dentition, and feeding preferences were also found to be subtle and difficult to generalise (Walter & Ikonen, 1989; Walter & Lindquist, 1989; Buryn & Brandl, 1992). Overall, the predictive power of available knowledge on the trophic ecology of individual species to higher taxonomic levels (genus or family) is limited (Walter & Ikonen, 1989). Notwithstanding, hypotheses of feeding guilds defined by ecological characteristics shared by species within given taxa, such as hunting behaviour or microhabitat preferences (Karg, 1989, 1993; Walter & Ikonen, 1989), are starting points for further research. For instance, small-bodied species living in deeper, mineral soil (e.g. some Rhodacaridae, Digamasellidae and Ascidae), but also larger species with long extendable chelicerae (e.g. many Uropodoidea), may be regarded as guilds feeding primarily on nematodes. Fast-moving and actively hunting taxa (e.g. some Veigaiidae, Parasitidae and Laelapidae) presumably utilising large amounts of microarthropod prey could represent one or more major trophic guilds among Mesostigmata in soil food webs. In any case, overall, trophic niches of Mesostigmata species have to be investigated in more detail, including the amount and relative composition of each specific prey type consumed in the field. This would permit better delineation of feeding guilds of soil-dwelling Mesostigmata and their role in soil food webs.

(*e*) *Pseudoscorpions*

Key message: *pseudoscorpions are generalist predators in the large mesofauna size class*, *feeding on a variety of arthropods*, *including other predators*.

Pseudoscorpions comprise 3500 species typically being of the size of large mesofauna taxa and occur in almost every terrestrial environment, but at low density and are well known for their ability to disperse *via* phoresy [Harvey, 1988 and references therein]. Some pseudoscorpion species use their chelicerae while others use their pedipalps with venom glands to catch prey (Gilbert, 1951). Pseudoscorpions feed on small arthropods such as springtails, thrips, mites, beetle larvae and flies (Harvey, 1988), but rarely on larger or more dangerous prey such as arthropods following use as phoretic vectors, other non-mite arachnids, woodlice, myriapods, mantids and ants (Tizo-Pedroso & Del-Claro, 2007; Del-Claro & Tizo-Pedroso, 2009; Garcia *et al*., 2016). Cannibalistic behaviour does not seem to be common in well-fed adults or animals of the same colony (Levi, 1948; Tizo-Pedroso & Del-Claro, 2007). Social species like the permanently social *Paratemnoides nidifikator* and *Paratemnus elongates* are often generalists able cooperatively to capture prey many times their own size (Zeh & Zeh, 1990; Tizo-Pedroso & Del-Claro, 2007; Garcia *et al.*, 2016), while solitary species may be more selective (Levi, 1948; De Andrade & Gnaspini, 2002). A few food-web studies (Scheu & Falca, 2000; Oelbermann & Scheu, 2010; Huang *et al.*, 2012; Pollierer, 2012) and one study focusing on pseudoscorpions (Liebke *et al.*, 2021) used stable isotope analysis to show that pseudoscorpions may be positioned high in the food web, suggesting that some species engage in intraguild predation and cannibalism.

(*f*) *Symphyla*

Key message: *Symphyla were shown to feed on plant roots*, *detritus*, *nematodes and small arthropods*, *thus are best classified as omnivores*.

Symphyla are small white myriapods mostly living in soil. Symphyla comprise two families, Scutigerellidae (ca. 128 species) and Scolopendrellidae (ca. 73 species) (Domínguez, 2009; Salazar-Moncada, Calle-Osorno & Ruiz-Lopez, 2015). They are found near the surface if growing plants are present, but if environmental conditions are unfavourable, they migrate downwards returning only upwards to feed (Edwards, 1959, 1961; Edwards, Lane & Nielsen, 2000). In organic-rich soils they can be abundant in the subsoil (30–60 cm depth), suggesting their association with roots and involvement in deep soil organic matter dynamics (Potapov *et al.*, 2017). Symphyla are prey of various soil predators (Menta & Remelli, 2020), but as a protection mechanism, they possess large spinnerets at the end of the body which emit sticky threads, entangling the mouthparts of predators. Feeding preferences in Symphyla differ among species (Scheller & Adis, 2002). Some species, like *Symphylella vulgaris*, presumably are exclusively saprophagous, while garden Symphyla may be crop pests. Only two genera in the family Scutigerellidae are considered to be pests for a wide range of crops: *Scutigerella* and *Hanseniella* (Michelbacher, 1938; Edwards, 1958). However, visual inspection of gut contents of *Symphylella* spp. showed that at least some species are predators on nematodes and small arthropods (Walter *et al.*, 1989). Existing data showed relatively high enrichment of Symphyla in ^{13}C and ^{15}N, suggesting that they live as microbivores or predators rather than herbivores (Potapov *et al.*, 2019b). Some data from arable systems also suggest them to live as predators (Albers, Schaefer & Scheu, 2006). Overall, the existing evidence suggests that Symphyla combine herbivory with feeding on detritus, nematodes and small arthropods. Due to limited information on species-specific differences, at present Symphyla are best classified as omnivores.

(*g*) *Pauropoda*

Key message: *pauropods are generalist detritivores and microbivores*, *feeding on fungi*, *plant roots and detritus in soil*. *Their feeding biology is poorly studied*.

Pauropoda are white, blind, cylindrical myriapods. With more than 900 species described, they occur worldwide, living in soil and decomposing litter, under bark and in mosses but usually at low densities in comparison to mites and springtails (Starling, 1944; Qian *et al.*, 2015; Rodrigez, 2015). They also serve as prey for various soil predators (e.g. spiders, centipedes, ground beetles and mites; Menta & Remelli, 2020). Generally, the mouthpart morphology of Pauropoda resembles that of diplopods suggesting that they are detritivores (Rodrigez, 2015). However, compared to millipedes they are small and inhabit deep soil layers, and the resources physically available to them are different (Starling, 1944; Potapov *et al.*, 2017). Early speculations suggested that the slow-moving species feed on decaying plant and animal material, whereas agile species consume microscopic animals (Latzel, 1883). However, empirical evidence suggests that they are decomposers rather than predators. Verhoeff (1934) found a species of *Pauropus* feeding on dead plant litter. Harrison (1914) observed *Paoropus carolinensis* to eat mould that grew on decaying leaf particles. In no instance, did they feed on dead animal material offered as food (Meyer & Scheller, 1992). Pauropoda were reported to feed on fungal hyphae and root hairs of plants (Starling, 1944; Hüther, 1959). The gut of Pauropoda contained hyphae (Rémy, 1950; Vašutová *et al.*, 2019), spores and plant tissues (Rémy, 1953; Rodrigez, 2015). However, unlike oribatid mites and springtails, Pauropoda are not favoured by high amounts of fungal biomass (Meyer & Scheller, 1992). Overall, Pauropoda can be considered to live as generalist detritivores or microbivores, feeding on fungi, plant roots and detritus, however, very little is known about their diet in the field.

(*h*) *Diplura*

Key message: *the diet of diplurans spans from living roots to detritus and fungi to other animals*. *Superfamily or family level of taxonomic identification reflects adaptations to certain foods*.

Diplura are basal hexapods, considered the sister group to insects and known as 'two-pronged bristletails' or 'doubletails' because of their two cerci at the hind end of the abdomen. All Diplura are terrestrial with a strong affinity for moist environments, and are found in soils and caves (Sendra, Palero & Jiménez-Valverde, 2020). They comprise more than 1000 extant species, divided into three well-distinguished subgroups, Campodeoidea, Projapygoidea and Japygoidea. Diplura share with proturans and springtails entognath mouthparts, but live more intensively as predators. Smaller Diplura are preyed upon by larger Diplura and other large arthropods, such as geophilid centipedes and ground beetles (Kosaroff, 1935; Gunn, 1992).

High feeding variety throughout different families can be explained by the shape of mandibular and maxillary structures (Bauer & Christian, 2007), and the type of cerci. Campodeoidea with up to 1 cm body length have long fragile multisegmented cerci, and mouthparts of grasping and crushing function. They live on various diets, from detritus and living plant roots to fungal hyphae and spores to other tiny invertebrates, and can be considered as detritivores or microbivores (Bareth, 1986; Gunn, 1992; Blesic, 1999; Bauer & Christian, 2007; Sendra *et al.*, 2021). Data on stable isotope ratios showed a high trophic level indicating that

Campodeoidea also may live partly as predators (Scheu & Falca, 2000; Potapov, Scheu & Tiunov, 2019a). Japygoidea range from 1.5 mm to 8 cm in body length and have unsegmented pincer-shaped cerci heavily sclerotised and with muscles suggesting an offensive or defensive role, and mouthparts optimised for perforating and tearing. These Diplura are mostly predators feeding on small arthropods such as mites, springtails, symphylans, insect larvae and also other Diplura, rarely woodlice, but also are known to feed on organic debris and fungal mycelia and spores (Pagés, 1951; Bauer & Christian, 2007; Sendra *et al.*, 2021). Within Japygidae, Heterojapygidae, Dinjapygidae and Gigasjapyginae are top invertebrate predators (Gonzalez, 1964), while Parajapygidae and perhaps Evalljapygidae species feed on plant roots including crops (Smith, 1960; Reddell, 1983). Projapygoidae are only a couple of millimeters long and have short multisegmented glandular cerci, probably with a defensive or offensive function. Within this subgroup Octostigmatidae have a plant diet (Rusek, 1982), but Projapygidae feed on microarthropods such as mites and pseudoscorpions (San Martín, 1963). Overall, various groups of Diplura play multiple roles in soil food webs – from species feeding on plant roots and living as detritivores to species feeding on fungi but also living as predators. However, only a few studies, especially those employing modern methods, have focused on the feeding habits of Diplura.

(*i*) *Protura*

Key message: *proturans are fungivores specialised on mycorrhizal fungi.*

Protura, also known as coneheads, are small soil-dwelling microarthropods that occur worldwide in soils, mosses, litter, and under bark and rocks (Nosek, 1977;Pass & Szucsich, 2011; Galli *et al.*, 2019). Proturans are considered microbivores in soil food webs (Galli *et al.*, 2019) and may serve as prey for small predators, such as spiders, mites and pseudoscorpions (Orgiazzi *et al.*, 2016). Proturans have stylet-like mandibles and maxillae, thus being well adapted to sucking. Sturm (1959) observed *Acerentomon gallicum* feeding exclusively by sucking on the outer coating of hyphae of ectotrophic mycorrhizae on oak and hornbeam roots. *Eosentomon transitorium* was observed sucking both on mycorrhizal fungi and an unidentified mycelium in soil (Sturm, 1959). These observations explain the frequent occurrence of Protura in the rhizosphere of trees with mycorrhiza. In laboratory cultures, proturans survive on mycorrhizal fungi, but also dead mites and mushroom powder (Tipping, 2008). In forest soil, the abundance of ectomycorrhizal fungi and Protura have been shown to be positively correlated (Pass & Szucsich, 2011; Galli *et al.*, 2019). A recent study based on stable isotope and fatty acid analyses confirmed that Protura are one of the rare invertebrate groups to specialise on ectomycorrhizal fungi as food source (Bluhm *et al.*, 2019). Thus, Protura can be classified as fungivores specialised in feeding on mycorrhizal fungi. The importance of other feeding strategies, such as feeding on saprotrophic fungi or necrovory needs to be evaluated in future studies.

(*j*) *Collembola*

Key message: *springtails are mainly microbivores and detritivores feeding on fungi, litter, algae and other microorganisms. Small and pale litter- and soil-dwelling species often occupy high trophic positions, while large and patterned surface-dwelling species are often linked to plant diets. These two groups also support different predators. Further classification into at least four trophic guilds is possible at the family level of taxonomic resolution.*

Collembola (springtails) are among the most abundant groups of soil mesofauna in virtually all terrestrial ecosystems with about 9000 described species (Bellinger, Christiansen & Janssens, 2020) and common densities of several dozens of thousands in temperate regions (Petersen & Luxton, 1982). Living in soil, litter and aboveground surfaces, they affect ecosystem functioning by shaping soil microbial communities and changing soil structure through litter comminution and casting (Faber & Verhoef, 1991; Maaß, Caruso & Rillig, 2015; Anslan, Bahram & Tedersoo, 2018; Coulibaly *et al.*, 2019). They play key roles in soil food webs as the connecting node between microorganisms and a wide range of invertebrate predators, spiders being the common example, as well as parasites and pathogens (Rusek, 1998). Many Collembola species feed on a wide range of food resources and are able to digest complex compounds, such as cellulose and chitin (Hopkin, 1997; Berg *et al.*, 2004). In laboratory cultures, Collembola often prefer dark-coloured fungi, but also feed on other small animals and benefit from mixed diets (Klironomos, Widden & Deslandes, 1992; Maraun *et al.*, 2003; Scheu & Folger, 2004; Chernova *et al.*, 2007). Fungal hyphae and amorphous plant material, 'humus', usually predominate in the gut of Collembola in forest soils, but many other food objects are present as well (Ponge, 2000; Addison, Trofymow & Marshall, 2003). In traditional soil food-web models Collembola typically are considered as fungivores (Hunt *et al.*, 1987; Moore, McCann & de Ruiter, 2005).

Stable isotope analysis revealed an unexpectedly high variation in trophic positions of Collembola, spanning from feeding on algae and plant litter to presumably feeding on other animals (Chahartaghi *et al.*, 2005; Ferlian *et al.*, 2015). Follow-up studies showed two main patterns in trophic-niche differentiation for Collembola: (*i*) species living near the litter surface (epedaphic life form) tend to feed on plant material, especially non-vascular plants, while species living in the soil (hemiedaphic and euedaphic life forms) feed on decomposed detritus, microorganisms or even microfauna (Hishi *et al.*, 2007; Potapov *et al.*, 2016b); (*ii*) species of Poduromorpha systematically occupy higher trophic positions than those of Entomobryomorpha and Symphypleona (Potapov *et al.*, 2016b). The soil depth-related differentiation in trophic niches confirmed earlier evidence from microscopic gut content observations that species living near the soil surface more often have pollen and algae in the gut, while the gut of species from deeper layers contains more humus and fungal material (Ponge, 2000). Despite high variation in enzymatic activity, near-surface-dwelling species have higher cellulase and chitinase activity, but lower trehalase activity than litter- and soil-dwelling species (Berg *et al.*, 2004; Potapov *et al.*, 2021a).

This suggests that species living near the surface predominantly graze on fungi and living vascular and non-vascular plants, or fresh litter, while species in deeper soil layers feed on organic matter decomposed by microorganisms or on root exudates. The Entomobryomorpha–Poduromorpha trophic distinction was also supported by fatty acid analysis (Ferlian *et al.*, 2015). Molecular analysis revealed low predictability of species-specific interactions between fungi and three epedaphic species of Collembola (Anslan *et al.*, 2018), suggesting that ecologically similar species may have similar feeding habits due to high trophic flexibility (Potapov *et al.*, 2019a). Across life forms and orders, body size and coloration are the two most informative traits to predict feeding habits of collembolan species: small and pale species are more likely to occupy high trophic positions, while large and patterned species are more likely to be linked to a plant diet (A. Potapov and T.-W. Chen, unpublished stable isotope analysis data).

Overall, Collembola can be easily separated into two feeding guilds. The 'surface guild' comprises large and coloured species (Symphypleona, surface-dwelling Entomobryidae, Tomoceridae), living near the surface or on ground vegetation, stones and bark. These Collembola feed on fresh litter, plants, fungi, pollen and non-vascular plants, with the proportion of algae and lichens likely being high (Potapov, Korotkevich & Tiunov, 2018). Despite being less abundant, surface-dwelling species may make a similar contribution to community biomass as soil-dwelling species in some ecosystems (Potapov *et al.*, 2018). Surface-dwelling species also likely serve as important prey for macropredators (McNabb, Halaj & Wise, 2001; Halaj & Wise, 2002). The 'soil guild' comprises pale and small soil-dwelling species, living inside the litter layer or mineral soil and feeding on decomposing detritus, colonised by both bacteria and fungi or are linked to rhizodeposits. Predators of these Collembola are also likely to be small in size and cryptic, for example mesostigmatic mites and other small predatory arachnids.

The simplistic two-guild classification proposed above has many nuances (Faber, 1991; Potapov *et al.*, 2016b). Numerically dominant species in most ecosystems are represented by the hemiedaphic life form and these species were shown to decline in the absence of root carbon (Fujii, Saitoh & Takeda, 2014). Close link to root carbon was repeatedly suggested for Onychiuridae, a soil-adapted family of Collembola (Endlweber, Ruess & Scheu, 2009; Fujii *et al.*, 2016; Potapov *et al.*, 2016a). However, the exact mechanisms of the trophic link between roots and Collembola remain unclear. While mycorrhizal fungi were suggested to play a major role (Pollierer *et al.*, 2012), direct feeding on mycorrhizal fungi is unlikely to represent the major trophic strategy for Collembola (Potapov & Tiunov, 2016; Bluhm *et al.*, 2019; Pollierer & Scheu, 2021). A distinct trophic position was also repeatedly recorded for Neanuridae, a family with piercing–sucking mouthparts (Chahartaghi *et al.*, 2005; Potapov *et al.*, 2016b). Stable isotope composition revealed that species within this family occupy high trophic positions, which was interpreted as feeding on nematodes or other microfauna (Chahartaghi *et al.*, 2005). There is also indication from laboratory cultures that they can feed on slime moulds, a widespread group of microbivorous protists (Hoskins *et al.*, 2015). Thus, Neanuridae can be considered high trophic level consumers, coupling the bacterial and fungal channels by feeding on other microbivores. Despite recent evidence based on compound-specific amino acid analysis that supports the assumption that Collembola predominantly live on saprotrophic fungi (Pollierer & Scheu, 2021), it is simplistic to consider Collembola to live uniformly as fungivores. As stressed increasingly, the bacterial and fungal channels are intimately interlinked in soil (de Vries & Caruso, 2016; Wolkovich, 2016), and labelling experiments and lipid profiles of Collembola suggest that they receive energy from both channels (Ngosong *et al.*, 2009; Crotty, Blackshaw & Murray, 2011; Ferlian *et al.*, 2015; Chen *et al.*, 2017).

Future studies need to link data on Collembola feeding habits with detailed descriptions of mandibular traits (Raymond-Léonard, Gravel & Handa, 2019) to verify the suggested differentiation in ecological functions of different species and groups. As a note of caution, however, the majority of information to date is from temperate forest and grassland ecosystems, while the tropics, tundra, arid and a number of other regions remain to be studied (but see Susanti *et al.*, 2021).

(3) Macroarthropods

(*a*) *Araneae*

Key message: spiders dominate predator communities in many terrestrial arthropod food webs with pronounced effects on prey populations and associated ecosystem functions. In soil food webs, most spider species are generalist feeders and particularly ground-active hunters affect Collembola densities and decomposition rates.

Araneae (spiders) are dominant predators in most terrestrial invertebrate food webs reaching an average biomass of 0.2 to 0.4 g m^{-2} in forest and grassland ecosystems worldwide (Nyffeler & Birkhofer, 2017). Globally, spiders kill an estimated biomass of 400–800 million tons of prey annually (Nyffeler & Birkhofer, 2017). Major prey orders of spiders in natural (Birkhofer & Wolters, 2012) and agricultural (Birkhofer, Entling & Lubin, 2013; Michalko, Pekár & Entling, 2019) habitats are Diptera, Hymenoptera, Coleoptera and Hemiptera. Spiders also feed on Collembola (Roubinet *et al.*, 2017), and in the tropics even attack and consume earthworms (Nyffeler *et al.*, 2001; Nyffeler & Birkhofer, 2017). Most species are opportunistic predators, but the proportion of prey items in diets often does not reflect the local prey availability, particularly for very abundant prey which is often underrepresented (Kuusk & Ekbom, 2012; Diehl *et al.*, 2013; Arvidsson *et al.*, 2020). Several spider species have evolved prey preferences, for example by specialising on woodlice in Dysderidae (Pekár, Coddington & Blackledge, 2012).

Spiders are excellent indicators of environmental change (Marc, Canard & Ysnel, 1999), as land-use intensification (Hanson *et al.*, 2017; Birkhofer *et al.*, 2017c), climate (Lensing, Todd & Wise, 2005; Wise & Lensing, 2019) or habitat heterogeneity (Sereda *et al.*, 2012) alter their taxonomic and functional composition. These community-level changes subsequently alter their functional role in invertebrate food webs (Birkhofer & Wolters, 2012; Mader *et al.*, 2016; Birkhofer *et al.*, 2017b). Predation by spiders affects decomposer communities and decomposition rates in forest ecosystems (Lawrence & Wise, 2004), contributes to pest control in agroecosystems (Birkhofer *et al.*, 2016a) and alters levels of intraguild predation in saltmarsh ecosystems (Finke & Denno, 2002). Observational studies of spider diets suffer from the fact that, in soil habitats, small, soft-skinned prey such as Collembola may be underestimated in the predator's diet (Birkhofer *et al.*, 2017a). Both web-building and ground-running spiders feed on soil animals. Prey groups such as Myriapoda (Yeargan, 1975; Smithers, 2005), Isopoda (Hódar & Sánchez-Piñero, 2002; Moya-Laraño *et al.*, 2002) or Collembola (Sunderland, Fraser & Dixon, 1986; Diehl *et al.*, 2013) can contribute more than 10% of all observed prey items. In an exclosure experiment, Wise (2004) reduced wolf spider densities by 50% in a forest floor ecosystem, resulting in a twofold increase in the abundance of tomocerid springtails. An increased availability of detrital resources to potential prey taxa from soil resulted in higher spider abundances in grasslands (Oelbermann, Langel & Scheu, 2008), but not in cereal fields (Birkhofer, Wolters & Diekötter, 2011b). (Micro) habitat complexity alters the effect strength of resource additions on the detritus–detiritvores–predator food chain in soils (Rickers, Langel & Scheu, 2006; Vucic-Pestic *et al.*, 2010; Birkhofer *et al.*, 2011b). Analyses of naturally occurring C and N stable isotopes in spiders and potential prey emphasise the role of large spider species as top predators in terrestrial food webs (Ponsard & Arditi, 2000) and the importance of detrital subsidy, presumably *via* Collembola prey, for spiders in agroecosystems (McNabb *et al.*, 2001; Wise, Moldenhauer & Halaj, 2006). Recent stable isotope studies further suggested that smaller spider individuals had stronger trophic links to soil-dwelling prey compared to larger individuals of the same species (Macé *et al.*, 2019; Murphy, Lewis & Wimp, 2020), and that the trophic position and diet composition of spider species varies across seasons (Radermacher *et al.*, 2020) and among farming systems (Birkhofer *et al.*, 2011a).

Molecular analyses of spider diets that considered soil fauna were initially motivated by the importance of (alternative) soil prey for spider species that provide biological control services (Agustí *et al.*, 2003; Kuusk & Ekbom, 2010). DNA-based analyses suggested that the diet of spider species can be stable across different environments (Eitzinger *et al.*, 2019; Zuev *et al.*, 2020), that farming systems and temporal dynamics affect diet composition (Roubinet *et al.*, 2017) and that spiders scavenge on prey carcasses (von Berg, Traugott & Scheu, 2012). Like stable isotope analyses, molecular methods suggest that (micro)habitat complexity strongly affects the functional role of spiders in local food webs (Michalko *et al.*, 2017; Staudacher *et al.*, 2018). Several recent papers refined molecular methods for diet analysis and provided new protocols to improve the detectability of prey DNA in spiders (Krehenwinkel *et al.*, 2017; Toju & Baba, 2018; Kennedy *et al.*, 2020).

In general, the majority of studies suggest that soil prey (Collembola in particular) are an important dietary component for ground-running (e.g. Lycosidae) and soil-based web-building species (e.g. Linyphiidae). To this end, a classification of spiders according to their main hunting guild may be the most promising method for simplified approaches to future soil food-web modelling (Uetz, Halaj & Cady, 1999; Cardoso *et al.*, 2011), as for example freely hunting species feed on Collembola more frequently than do web-building species (Birkhofer & Wolters, 2012). Stalking and ambushing spider species or species with sheet webs frequently catch mobile prey, while active hunters commonly feed on sedentary prey [e.g. aphids (Birkhofer *et al.*, 2008; Michalko *et al.*, 2019)]. However, the stratum preference and body size of spider species further determines diet composition (Birkhofer *et al.*, 2013). The combination of different methods of diet analyses will be a powerful approach to improve these classifications based on trophic ecology of spiders in soil food webs in the future (Birkhofer *et al.*, 2008; Furlong *et al.*, 2014; Hambäck *et al.*, 2016; Kennedy *et al.*, 2019). Classifications based on multiple traits, including body size, hunting mode and phenology are additional methods that may contribute to a more refined classification of subsets of species with similar feeding preferences.

(*b*) *Opiliones and other predatory arachnids*

Key message: harvestmen are generalistic surface-dwelling predators, but are known for scavenging and also may supplement their diet with plant food. In subtropical, tropical and arid ecosystems several other groups of predatory arachnids are present, but knowledge on their role in soil food webs is scarce.

Opiliones (harvestmen) are the most common arachnids after spiders and mites with approximately 6700 species described (Giribet & Sharma, 2015; Kury *et al.*, 2021). They can be found from boreal and temperate to tropical ecosystems, and are often associated with leaf litter, various ground surfaces and vegetation. They are preyed upon by various vertebrates and invertebrates (Pinto-da-Rocha, Machado & Giribet, 2007; Powell *et al.*, 2021), and to protect themselves from predation use various strategies, including crypsis, mimicry, thanatosis and leg autotomy (Pinto-da-Rocha *et al.*, 2007). Unlike most other predatory arachnids, Opiliones have the ability to masticate and ingest solid food; they supplement animal prey with palatable plant material like fruits, thus being in part omnivorous (Halaj & Cady, 2000; Agosta & Machado, 2007; Schaus, Townsend Jr & Illinik, 2013). Opiliones are more active at night and feed on various insects and other arachnids, springtails, woodlice, millipedes and also on oligochaetes and gastropods (Adams, 1984; Halaj & Cady, 2000;Agosta & Machado, 2007; Powell *et al.*, 2021). Soil-associated Opiliones use a sticky apparatus on the pedipalps to capture springtails (Wolff *et al.*, 2014). A serological survey suggested that temperate forest Opiliones use Diptera as their main prey, however, this was only one of many prey groups consumed (Adams, 1984). Opiliones feed on gastropods, with some species even specialising on them (Nyffeler & Symondson, 2001). Opiliones are also known to feed on earthworms in arable fields (Halaj & Cady, 2000) and in forests (Adams, 1984), however, this trophic link may represent scavenging rather than predation (Halaj & Cady, 2000; Powell *et al.*, 2021). Dead invertebrates in general are an important part of the diet of many Opiliones, widening the range of the food items consumed (Agosta & Machado, 2007; Powell *et al.*, 2021). Novel methods have rarely been applied to study the feeding habits of Opiliones; the few existing stable isotope data suggest that Opiliones occupy a slightly lower trophic level than other arthropod generalist predators (de Hart & Strand, 2012; Korobushkin, Gongalsky & Tiunov, 2014; Potapov *et al.*, 2019b), confirming their partial omnivory. As revealed by diagnostic PCR, Opiliones combine feeding on aboveground (moth larvae) and soil-associated prey (springtails) in agricultural landscapes (Papura *et al.*, 2020). Further studies revealing the contribution of below- and aboveground prey in the diet of Opiliones are needed to understand their role better in soil food webs.

Apart from Opiliones, several less species-rich predatory groups of arachnids are involved in soil food webs in certain habitats, for example in subtropical and tropical humid environments (Scorpiones, Thelyphonida, Amblypygi, Schizomida, Palpigradi) or arid ecosystems (Scorpiones, Solifugae) (Harvey, 2003). While Palpigradi and Schizomida are mostly small (up to 5 mm) and pale soil- and cave-associated groups, other taxa are large active or sit-and-wait predators that feed on various ground micro- and macroarthropods in their own size range. A high trophic level for Scorpiones in tropical forest soils was confirmed by stable isotope data, and even small-sized Amblypygi may occupy a very high trophic position in tropical forest soil food webs (Kupfer *et al.*, 2006; Semenina *et al.*, 2020). The roles of these groups in the context of soil food webs are poorly known, mostly due to overall limited knowledge on tropical soil communities.

(*c*) *Diplopoda*

Key message: *millipedes are mainly detritivores feeding on decaying plant material colonised by microorganisms. In species-rich tropical millipede communities trophic niche differentiation among species has been observed. Trophic position of millipede species is rarely predictable by phylogeny, but correlates with microhabitat preferences of species.*

Diplopoda (millipedes) are abundant detritivores of medium to large size with *ca.* 8000 species described and an affinity to forest ecosystems, especially tropical ones (Shelley & Golovatch, 2011) where the local fauna may exceed 100 species (Golovatch, Tiunov & Anichkin, 2011). Diplopoda are characterised by a rather uniform body plan, but different morphotypes reflect adaptations to life under or on the bark of trees, in litter or in soil (Golovatch & Kime, 2009). The main ecosystem role of Diplopoda is functioning as 'litter transformers' (Lavelle & Spain, 2001). Diplopoda may consume a significant fraction of the annual litterfall: depending on the ecosystem it is usually in the first dozens of per cent, but may be up to 40% (Dangerfield & Milner, 1996; Lawrence, 1999; Cárcamo *et al.*, 2000; González, Murphy & Belén, 2012). Diplopoda are involved in the first stages of plant litter decomposition; they macerate leaf litter and excrete still palatable material due to low assimilation rates (David & Gillon, 2002). This excreta is enriched with microflora, thereby speeding up decomposition processes (Anderson & Bignell, 1980; Kaneko, 2009; Joly *et al.*, 2020). However, some studies showed that decomposition of the litter enclosed in faecal pellets may be slower (Nicholson, Bocock & Heal, 1966; Webb, 1977; Scheu & Wolters, 1991; Suzuki, Grayston & Prescott, 2013). Despite high biomass, Diplopoda play a minor role as food for predators due to anti-predatory adaptations. Vertebrates rarely consume them (Baker, 1985; Hendra, 1999; Jedlicka, Sharma & Almeida, 2013) partly because of their poison glands. However, some invertebrate predators, like assassin bugs, ants and beetles, are specialised on Diplopoda (Brunke *et al.*, 2009; Forthman & Weirauch, 2012).

The trophic ecology of Diplopoda is well covered in the key myriapodology books of Hopkin & Read (1992) and Minelli (2015), which refer to them as generalists feeding on leaf litter colonised by fungi and bacteria. However, some species, genera and families have more specific diets, such as fungal mycelia, algae films, animal remains, other animals or crops (Srivastava & Srivastava, 1967; Hoffman & Payne, 1969; Ebregt *et al.*, 2005; Read & Enghoff, 2009). Diplopoda have a rather simple digestive system with large amounts of symbiotic microflora (Hopkin & Read, 1992) that produce cellulases facilitating the digestion of plant materials (Byzov, 2006; Farfan, 2010). In many laboratory experiments Diplopoda preferred certain kinds of food materials from a given choice (Bertrand & Lumaret, 1992; Svyrydchenko & Brygadyrenko, 2014), but under natural conditions their diet may be much wider (Hoffman & Payne, 1969; Wooten & Crawford, 1975).

Novel methods have provided information about the diet of Diplopoda *in situ*. Analysis of the stable isotope composition of C and N confirmed that Diplopoda are detritivores assimilating microflora rather than the plant material itself, and showed the wide range of species' trophic niches (Pollierer *et al.*, 2009; Semenyuk & Tiunov, 2011b; Potapov *et al.*, 2019b). Even communities comprising only a few species, such as those in leaf litter in temperate regions, support species with different trophic niches including primary and secondary decomposers (Scheu & Falca, 2000; Oelbermann & Scheu, 2010), and species with specific ecology (and trophic niches), such as some Nemasomatidae species associated with decaying wood or Polyzoniidae species associated with leaf litter highly colonised by fungi and microorganism-rich liquids (David & Vannier, 1996; Semenyuk & Tiunov, 2011a). Species in more diverse subtropical and tropical Diplopoda communities use a wider range of feeding strategies, partly due to the absence of a permanent leaf litter layer creating the need to use other resources (Dangerfield & Kaunda, 1994; Golovatch & Kime, 2009). In tropical ecosystems, species are separated into different trophic guilds including leaf litter feeders, algae feeders and soil/protein-enriched substrate feeders (Semenyuk, Tiunov & Golovatch, 2011). Some species switch their diet from leaf litter to algae films/lichens and back depending on the season (I. Semenyuk, unpublished data).

The ecology of Diplopoda species (including their trophic position) is not closely associated with their phylogeny; only Colobognatha are considered fluid feeders, likely by sucking on fungal hyphae or algae films (Read & Enghoff, 2009; Moritz *et al.*, 2021). In specific cases, feeding is linked to the species' life history and spatial preferences such as in Polyxenidae which feed on algae/lichen films and crusts, but life history is not known for most species (Alexander, 2012; Semenyuk & Tiunov, 2019).

Surprisingly, novel methods have been underused for investigating the ecology of Diplopoda despite the lack of understanding of their trophic position in communities, especially in tropical and subtropical regions. In most studies Diplopoda of only medium size have been included (1–4 cm body length), while smaller species (1–5 mm) and more importantly juveniles, which form a large part of the biomass, usually have been ignored. The ecology of juveniles may differ from that of adults (Toyota, Kaneko & Ito, 2006). For example, by labelling trees with ^{13}C and ^{15}N it was shown that early developing stages of typical saprotroph Polydesmidae may feed on fine roots (Zieger, 2015). Other studies also indicated age-related changes in trophic niches of millipedes (Potapov, Semenyuk & Tiunov, 2014). A serious problem is that considerable further taxonomic work is needed to allow identification of species and that there are only few field guides and keys, especially for tropical regions. The development of technologies also allowing identification of juveniles is an important step to foster an understanding of the position of Diplopoda in soil food webs.

(*d*) *Chilopoda*

Key message: *centipedes are predators feeding on a wide spectrum of meso- and macrofauna, and often are linked to the root-based energy channel. Centipede groups differ in morphology, which is related to different microhabitat and feeding preferences. Niche partitioning among species depends on predator–prey body size ratios, habitat structure and prey availability.*

Chilopoda (centipedes) are important predators in many terrestrial food webs (Poser, 1988; Lewis, 2006; Voigtländer, 2012). They comprise *ca.* 3300 species belonging to the five major groups Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha and Geophilomorpha (Edgecombe & Giribet, 2007). Chilopoda mostly live in leaf litter or soil, or hide under stones and bark, often preferring moist habitats (Voigtländer, 2012). Based on their locomotion, Manton (1977) described three ecomorphotypes or life forms that occupy different habitats. The burrowing type comprises Geophilomorpha with an elongated body living in deeper soil layers. The intermediate type comprises Scolopendromorpha and Craterostigmomorpha, which are able to move fast, but also to dig deep, branched burrow systems. Finally, the running type comprising the fast-running Scutigeromorpha that hunt on open surfaces, and the Lithobiomorpha with a flattened body, which hunt in leaf litter, the upper soil layer and under stones and bark. Chilopoda have different foraging strategies, including sit-and-wait predators and active hunters. The former are often found in Lithobiidae (Poser, 1988; Guizze *et al.*, 2016), whereas, others such as Scolopendromorpha usually actively hunt their prey. However, their strategies may change according to prey density and size (Formanowicz & Bradley, 1987; Günther *et al.*, 2014).

Food choice experiments and visual gut content analyses suggest that Chilopoda prey on a wide range of animals, including decomposer invertebrates such as springtails and earthworms, but also spiders and other Chilopoda (Hickerson, Anthony & Walton, 2005), or in case of Scolopendromorpha even amphibians, newborn mice and bats (Molinari *et al.*, 2005; Srbek-Araujo *et al.*, 2012; Guizze *et al.*, 2016). Littoral Geophilomorpha species feed on barnacles and periwinkles (Blower, 1957), suggesting that Geophilomorpha potentially feed on Gastropoda in leaf litter as well.

Bulk stable isotope analysis of Lithobiomorpha and Geophilomorpha indicate that they are mainly predators of primary and secondary decomposers (Scheu & Falca, 2000; Pollierer *et al.*, 2009). High inter-individual variation in isotopic composition (^{13}C and ^{15}N) indicates that their prey spectrum may be highly variable even within species (Klarner *et al.*, 2017). Trophic flexibility may allow Chilopoda to cope with differing environmental conditions occurring in different forest types (Ferlian & Scheu, 2014), and with land-use change (Günther *et al.*, 2014; Klarner *et al.*, 2017).

Nevertheless, combined analyses of stable isotope values and fatty acid patterns suggest that different species of Chilopoda occupy distinct trophic niches, which are linked to different basal resources and can change during maturation (Ferlian, Scheu & Pollierer, 2012). For instance, *Strigamia acuminata* (Geophilomorpha) was more closely associated with the bacterial energy channel, whereas Lithobiomorpha relied more on the fungal energy channel (Ferlian, Scheu & Pollierer, 2012). Labelling experiments confirmed fungi as a basal resource and suggested that lithobiid Chilopoda are strongly linked to root-derived carbon (Pollierer *et al.*, 2012; Eissfeller *et al.*, 2013; Goncharov *et al.*, 2016), potentially *via* feeding on Collembola or Lumbricidae, which can be a major prey for Lithobiidae (Günther *et al.*, 2014; M.M. Pollierer and V. Krashevska, unpublished data) and can acquire carbon from roots (Pollierer *et al.*, 2007; Li *et al.*, 2020).

Distinct trophic niches of co-occurring Chilopoda species were confirmed by molecular gut content analyses, for example in Geophilomorpha and Lithobiidae (Bortolin, Fusco & Bonato, 2018). Presumably, predator–prey body size ratios in combination with habitat structure play an important role in trophic niche partitioning in Chilopoda (Schneider, Scheu & Brose, 2012; Kalinkat, Brose & Rall, 2013; Günther *et al.*, 2014). For instance, while larger *Lithobius mutabilis* captured fewer springtails in thick layers of leaf litter due to prey dilution effects, the smaller species *Lithobius crassipes* benefited from higher amounts of leaf litter, presumably due to competitive release from larger predators and adaptations to hunt in smaller crevices (Günther *et al.*, 2014). Increasing resource availability is assumed to exert bottom-up effects on Chilopoda (Salamon *et al.*, 2006), while diminishing top-down effects on their springtail prey (Kalinkat *et al.*, 2013).

Overall, when reconstructing food webs, Chilopoda can be classified as typical predators. However, there is a wide variability of prey, differing among orders, families, species or even within species of Chilopoda. Differences in prey spectra depend on life forms (ecomorphotypes), as these occupy different habitats and follow different foraging strategies, but the diet also depends on body size and age. Further, the diet may differ between the same species in different environments, such as differently managed forests. These factors, together with the availability of prey, must be taken into account when integrating Chilopoda into soil food-web models. Novel methods, such as compound-specific analyses of amino acids (^{15}N and ^{13}C) (Pollierer *et al.*, 2019), may allow more detailed insights into the trophic positions and basal resources of Chilopoda across different life forms and habitats, thereby promoting our understanding of trophic niche partitioning in this important group of predators.

(*e*) *Isopoda*

Key message: *woodlice are generalist detritivores with frequent coprophagy. They are able to shift their diet depending on resource quality and utilise detrital compounds, such as lignocellulose, with the help of a rich gut microbiome. No trophic guilds within the group are currently recognised.*

Oniscidea (woodlice) are the only group of widespread terrestrial crustaceans (Sutton, 2013) with over 4000 species (Schmalfuss, 2003). Woodlice are saprophagous and possess uniform chewing mouthparts (Vandel, 1960). If abundant, as for example in broadleaved forests (Gongalsky *et al.*, 2005; Kuznetsova & Gongalsky, 2012), woodlice play an important role in litter decomposition. Across ecosystems, they typically consume 1–4% of the annual litter material, but in addition to litter they also ingest mineral soil (Pok, 1976). Woodlice serve as food for large invertebrate predators, like carabids (Sergeeva & Gruntal, 1988) or spiders (Rezác, Pekar & Lubin, 2008). Since they are well armoured they mainly are hunted by predators larger in size.

Woodlice eat both leaf litter and rotting wood, and in addition they also consume animal tissue. In desert species, phytophagy represents an adaptation to moisture deficit in the arid climate (Shachak, Chapman & Steinberger, 1976; Krivolutsky, Pokarzhevskii & Sizova, 1985). This occasionally may also occur in agricultural ecosystems (Boer, 1962). First evidence that woodlice feed on microorganisms came from the fact that they eat their own faeces (Hassall & Rushton, 1985). Coprophagy in woodlice, apparently, has the same function as coprophagy in mammals, namely the use of microbial proteins rich in essential amino acids. This is indicated by a large proportion of the diet based on substrates with poor microbial colonisation, such as fresh or contaminated litter (Hassall & Rushton, 1985). Modelling of elemental and isotopic mass balances indicated that faeces recycling explains the unexpected high ^{15}N enrichment in the isopod *Porcellio dilatatus* (Rothe & Gleixner, 2000).

The digestive system of Isopoda is complex and serves multiple functions such as food processing, absorption and storage of nutrients, synthesis of digestive enzymes and blood proteins, detoxification of xenobiotics and osmoregulation (Štrus *et al.*, 2019). Since their nutrition is based on plant detritus, it has long been suspected that bacterial symbionts located in the gut might play an important role in host nutrition *via* the provisioning of digestive enzymes, thereby enabling the utilisation of recalcitrant food compounds such as cellulose and lignin. The gut bacterial community of Isopoda varies in different populations, suggesting an important effect of the environment on the host-associated microbiota (Bouchon, Zimmer & Dittmer, 2016; Bredon *et al.*, 2019). Apart from plant detritus, saprotrophic fungi were shown to be a major food resource for some woodlice, for example *Oniscus asellus* (A'Bear *et al.*, 2014). Even at low density woodlice may reduce mycelial biomass and alter competitive interactions among fungal species (Crowther, Boddy & Jones, 2011; Crowther *et al.*, 2013).

Early studies using natural variations in stable isotope ratios suggested that the trophic position of isopod species may vary over a range equivalent to about one trophic level, reflecting that some species predominantly feed on plant material (leaf litter) thereby functioning as primary decomposers, whereas others predominantly consume microorganisms thereby functioning as secondary decomposers (Scheu & Falca, 2000). Interestingly, the former comprised large species such as *Porcellium conspersum*, whereas the latter comprised small species such as *Trichoniscus pusillus*. Recently, Bluhm *et al.* (2021) used lipid analysis to confirm that *T. pusillus* feed predominantly on microorganisms and suggested this species to be among the very few that could switch its diet towards bacteria in experiments severing the input of root-derived resources by root trenching.

Although it has been documented that woodlice consume both plant litter as well as microbial resources with the relative importance of these varying among species, to date woodlice have not been grouped into trophic guilds, presumably because most woodlice species are able to feed on a broad variety of resources. Potentially, however, food preferences vary with body size. This likely affects the size spectrum of their food, with large species able to feed on larger and harder plant material, while small species may feed more on microorganisms. To date there are no data documenting the extent to which different food resources (plant litter, fungi, bacteria) constitute the diet of woodlice under different environmental conditions. Thus, future research should focus on (*i*) the general relationship between resource quality and feeding strategies in woodlice, and (*ii*) exploring the feeding habits of different size classes, especially small species.

(*f*) *Dermaptera*

Key message: *earwigs are omnivores feeding on living and dead plant and animal material*; *mouthpart morphology can be used to distinguish species with preferences for animal diets*.

Dermaptera (earwigs) are one of a species-poor insect order comprising about 1900 described species (Hopkins *et al.*, 2018; Wipfler *et al.*, 2020) mainly distributed in warm and wet tropical areas (Ha, 2018). Dermaptera occur in the litter layer, under stones and decaying trees, on herbs, shrubs and trees, and are abundant in agroecosystems (Powell, 2009; Kacar & Nishikawa, 2014; Orpet, Crowder & Jones, 2019). Dermaptera have chewing mouthparts allowing them to consume hard food. Their diet typically consists of a wide array of living and dead plant and animal material (Powell, 2009; Kirstová, Pyszko & Kocarek, 2018). In turn, they are preyed upon by a variety of predators including spiders, centipedes and assassin bugs, and are parasitised by for example flies, astigmatid mites, nematodes and parasitoid wasps. To protect themselves against predators they use pincers and some species produce defensive secretions.

Most Dermaptera are omnivores with a low degree of diet specialisation (Toups *et al.*, 2008; Powell, 2009; Quarrell, Corkrey & Allen, 2017; Orpet *et al.*, 2019). Commonly observed food in the gut of the European earwig *Forficula auricularia* is of both plant and animal origin, including moss, grass, lichen and aphids (Crumb, Bonn & Eide, 1941). In agroecosystems this species has been reported to eat both fruits and a variety of pests including midge larvae, hemipterans and butterfly eggs and larvae, aphids and psyllids (Orpet *et al.*, 2019). Mouthpart morphology can be useful to assess the trophic position of Dermaptera species (Coll & Guershon, 2002). In carnivorous species the incisive area occupies two thirds of the total mandibular length, while it is restricted to half the mandibular length in phytophagous and omnivorous species (Waller, Caussanel & Jamet, 1996). The few existing stable isotope data revealed high variability within and among species (Okuzaki *et al.*, 2009), confirming an omnivorous diet with a wide range of consumed resources and diet switching. The contribution of Dermaptera to the decomposition of plant debris in soil is small even at high densities (Striganova, 2017). Dermaptera can be considered omnivorous, but mouthpart morphology may be used for more detailed classification.

(*g*) *Orthoptera*

Key message: *orthopterans are divided into Caelifera and Ensifera with Caelifera being predominantly herbivores*, *while Ensifera includes herbivores*, *predators and omnivores*, *which may be distinguished based on family-level identification*.

With about 26,000 known species, Orthoptera can be found from soil to canopies across terrestrial habitats outside polar regions (Song, 2018). Orthoptera are divided into Caelifera and Ensifera, the latter with long antennae (Grylloidea, Gryllotalpoidaea, Tettigonoodae, Raphidophoroidea, Schizodactyloidea), the former with short antennae (Tetrigoidea, Tridactyloidea and Acridoidea) (Resh & Cardé, 2009; Song *et al.*, 2015). Both groups, depending on taxon, size and lifestyle, are preyed upon by various vertebrates (e.g. eulipotyphlan mammals, bats, birds, lizards) and invertebrates (e.g. spiders, predatory beetles and other Orthoptera). As a defence against predators, Orthoptera use various mechanisms such as jumping, mimicry, fighting, and even feed on toxic plants and use secondary plant compounds for their own defence (Song, 2018).

Caelifera are not typical members of the detrital food web since they primarily consume living plant material, however, according to stable isotope analysis, these grazers are involved in soil food webs as prey for litter predators such as spiders (Halaj, Peck & Niwa, 2005). Within Caelifera, Tetrigidae (pygmy grasshoppers) live on the soil surface and are directly involved in soil food webs by feeding on microalgae growing on moist soils, mosses, humus or detritus (Bastow *et al.*, 2002; Karpestam & Forsman, 2011, 2013). Phycophagy of larval stages of Tetrigidae was confirmed by stable isotope analysis (Semenina *et al.*, 2020).

The diet of Ensifera varies widely (Song, 2018). Most crickets (Gryllidae, Ensifera) are omnivorous, feeding on detritus, dead insects and plants (Kevan, 1982; Resh & Cardé, 2009). Mole crickets (Gryllotalpidae and Cylindrachetidae) have wide forelegs, modified for burrowing and create tunnels and galleries in soil (Frank & Parkman, 1999). These animals are also omnivorous and feed on plant roots and litter, but also on invertebrate larvae and earthworms. Stable isotope composition (^{13}C and ^{15}N) of *Gryllotalpa unispina* in a West Siberia dry ecosystem resembled that of predatory carabid beetles, suggesting that animal food predominates in its diet (Lyubechanskii *et al.*, 2015). Some basal Ensifera, including Anostostomatidae, Gryllacrididae, Rhaphidophoridae and Stenopelmatidae, are scavengers or predators of small insects (Field, 2001; Song, 2018). Several subfamilies of Tettigoniidae are obligate predators with spined tibiae modified for capturing prey (Bailey & Rentz, 1990).

Orthoptera is a well-studied group as crop pests, but is much less investigated in its role as a link between above- and belowground food webs. Herbivorous Caelifera are prey for different ground predators, while predatory Ensifera species feed on invertebrates on the soil surface. During outbreaks of Orthoptera (locusts and grasshoppers) carcasses serve as large influx of nutrients over a relatively short period of time, that increased nutrient content in detritus (primarily N) and microbial respiration, resulting in bottom-up effects on primary productivity that may in part counteract their negative impact on plants (Hawlena *et al.*, 2012; Song *et al.*, 2015; Ohgushi, Wurst & Johnson, 2018). Overall, Orthoptera are classified as predators, herbivores or omnivores at order and family level. Further research may focus on Orthoptera as important linking agents between above- and belowground food webs.

(*h*) *Embioptera*

Key message: *webspinners are gregarious insects that build silk domiciles for protection and foraging. They feed mainly on algae and lichens*, *but also consume detritus*.

Embioptera (webspinners) is a small order of insects with less than 460 described species (Engel & Grimaldi, 2006).

Embioptera are most diverse in tropical and subtropical regions, but also occur in the Mediterranean and in other semi-arid regions (Ross, 2000; Szumik, Edgerly & Hayashi, 2008). Embioptera are about 1–2 cm in length, gregarious and live subsocially in galleries of fine silk, which they spin from glands on their forelegs. Their unarmoured body leaves embiids especially vulnerable to predation by for example ants, spiders and parasitoid wasps (Sclerogibbidae). Silk domiciles and other constructions may protect Embioptera from predators, but also are important for thermoregulation. Silk-covered foraging zones are extended as individuals seek food (Edgerly, Davilla & Schoenfeld, 2002). In the field, silk of large Embioptera may cover entire tree trunks, reaching up to 37,000 cm^2 in area (Edgerly, 1987). Embioptera have chewing mouthparts (Ross, 2008) and mainly feed on lichens and algae, but also on detritus (Edgerly *et al.*, 2002; Edgerly, Tadimalla & Dahlhoff, 2005). Very low δ^{15}N values suggest that in Mediterranean ecosystems Embioptera (*Haploembia solieri*) function primarily as phycophages feeding on algae and lichens (D. Korobushkin, unpublished stable isotope analysis data). Overall, the participation of webspinners in soil food webs and their influence on soil ecosystems by constructing silk galleries require further research.

(*i*) *Blattodea (except Isoptera)*

Key message: *cockroaches feed on a wide variety of food resources and are opportunistic in their food choice. In natural environments they primarily function as detritivores, feeding on leaf litter and rotten wood.*

Cockroaches include about 4640 species (Beccaloni & Eggleton, 2013) and are most abundant in tropical and subtropical climates, but are also found in temperate and boreal regions. Along with termites (Isoptera), they are included in the order Blattodea, and harbour complex gut microbiomes that aid in the breakdown of recalcitrant dietary substrates including cellulose (Bell, Roth & Nalepa, 2007). Synanthropic species are well known, but more than 95% of all species of cockroaches live in natural habitats (Brenner & Kramer, 2019). They are present in nearly all ecosystems including forests, grasslands, wetlands, coasts and deserts (Bell *et al.*, 2007). In tropical ecosystems cockroaches are among the most important soil invertebrates, responsible for the breakdown of leaf litter and wood together with termites, earthworms and millipedes (Tiunov, 2011; Cipola & Dias Tarli, 2019). Cockroaches form prey for a variety of macroinvertebrates, such as spiders, carabids and scorpions, and vertebrate predators, such as birds, lizards and frogs (Smith, Beard & Shiels, 2016). To avoid predation, some cockroaches have camouflaged and sclerotised forewings, the nymphs of some species secrete a proteinaceous protectant, while the eggs of most cockroaches are protected by ootheca (Bell *et al.*, 2007).

Cockroaches are good survivors and opportunists. The distribution of cockroach individuals is often correlated with the proximity of appropriate food sources (Basset *et al.*, 2003; Bell *et al.*, 2007). For example, in sparsely vegetated sites cockroaches are frequently associated with vegetation and detritus patches, independent of plant species (e.g. Sinclair, 2001). Most cockroaches are highly mobile and exhibit daily and seasonal movements in response to their dietary, reproductive and microenvironmental needs (Bell *et al.*, 2007).

Cockroaches are typically described as omnivores, scavengers or ‘classic generalists’. Information on the contribution of cockroaches to litter decomposition is scarce and complicated by their opportunistic feeding (Dow, 1987; Bell *et al.*, 2007; McCue, 2008). Leaf litter particles usually dominate in the gut of cockroaches, but they also ingest microorganisms and microfauna or even other juvenile cockroaches (Bell *et al.*, 2007). Cockroaches are at least partly herbivorous, occasionally feeding on pollen, nectar, sap, roots, bark, flowers and fruits (Bell *et al.*, 2007). There is also an important group of xylophagous cockroaches (e.g. genus *Cryptocercus*, *Parasphaeria*, *Salganea*) some of which show termite-like subsociality (biparental family groups) and live in the interior of rotten logs, inhabiting galleries they have chewed into the dead wood (Klass, Nalepa & Lo, 2008; Nalepa, 2020). A prominent feature uniting wood-feeding cockroaches (e.g. genus *Cryptocercus*, *Parasphaeria boleiriana*) with termites is a mutualistic relationship with single-celled anaerobic eukaryotes (protists, flagellates) that live in an enlarged hindgut paunch of the insects (Pellens *et al.*, 2007; Klass *et al.*, 2008).

The few data existing on stable isotope composition from both temperate and subtropical areas confirmed that cockroaches are mainly detritivores feeding on dead plant and animal material (Okuzaki *et al.*, 2009; Colombini *et al.*, 2011; Goncharov *et al.*, 2011; Korobushkin *et al.*, 2016). The gut microorganisms of cockroaches are involved in the digestion of food materials and the production of volatile fatty acids and other metabolites that modulate development, nutritional status, and communication of their host (Kane & Breznak, 1991; Wada-Katsumata *et al.*, 2015; Kakumanu *et al.*, 2018).

Overall, cockroaches can be considered opportunistic detritivores feeding on plant detritus (litter and rotten wood). Their high mobility suggests that they play an important role in the redistribution of spatial energy and nutrients in the ecosystem. While extensive work has been carried out on synanthropic species, knowledge on the functional role of cockroaches in food webs of tropical ecosystems where they can reach high biomass is scarce (Nalepa *et al.*, 2002; Bell *et al.*, 2007; Cipola & Dias Tarli, 2019).

(*j*) *Isoptera*

Key message: *termites are social insects that are highly abundant in the tropics and subtropics, and act as decomposers feeding on grass, wood, litter and soil. They are effective in digesting complex plant tissues with the help of mutualistic organisms and are classified into four trophic groups according to the decomposition stage of their food.*

Termitoidae (termites) are diverse and abundant eusocial insects, found mostly in subtropical and tropical forests and savannas. There are about 3100 species of termites (Constantino, 2016). The biomass of termites can reach up to 40–60% of the entire macrofaunal biomass in tropical soils

(Dahlsjö *et al.*, 2014). The main ecological role of termites is decomposition of plant organic matter, such as wood or litter in various stages of decay. With the help of an array of gut symbionts, termite-produced enzymes or exo-symbiotic fungi, termites can assimilate up to 74–99% of the ingested cellulose and up to 83% of the ingested lignin (Watanabe & Tokuda, 2010). With such effective digestion, termites emit significant amounts of methane and carbon dioxide into the atmosphere (Sanderson, 1996). Some termite species build soil nests and protective structures, thereby substantially contributing to soil bioturbation and by nest space provisioning to soil biodiversity (Visser, Freymann & Schnyder, 2008; Hood *et al.*, 2020).

Termites are detritivores feeding mainly on plant-based materials including dead wood, leaf litter, grasses and soil varying in organic matter content (Donovan, Eggleton & Bignell, 2001). Less typical food includes epiphytic lichens, mammalian dung and vertebrate carcasses (Eggleton & Tayasu, 2001; Prestes *et al.*, 2014; Barbosa-Silva & Vasconcellos, 2019). Phylogenetically basal termites, 'lower termites', such as Rhinotermitidae and Kalotermitidae, feed on dead wood or grass as a primary food source, and digest it with the help of symbiotic protists in their gut. Phylogenetically more advanced 'higher termites' (Termitidae) lost their gut symbiotic protists. Instead, lignocellulose is processed by their own enzymes, diverse bacterial communities living in the morphologically complex gut or by fungi of the genus *Termitomyces* grown by macrotermitid termites in their nests (Abe, Bignell & Highasi, 2000).

Termites are important prey for a wide spectrum of predators (Deligne, Quennedey & Blum, 1981). They often are abundant and their poorly sclerotised bodies, especially in the worker caste and winged reproductives, are valuable sources of energy (Wood & Sands, 1978). Mammals, such as pangolins, anteaters or sloth bears, are effective termite predators. A range of lizards, birds and invertebrates also attack termites (Deligne *et al.*, 1981; Pianka, 1986). However, the most important termite predators are ants (Hölldobler & Wilson, 1990). There are both generalist termite-preying ants such as *Pheidole* spp., and highly specialised species able to disrupt termite colonies such as *Neoponera* spp. (Tuma, Eggleton & Fayle, 2020). Predation on termites can slow down ecosystem processes supported by termites such as plant litter decomposition and bioturbation (DeSouza, Araújo & Reis-Jr, 2009; Ashton *et al.*, 2019; Tuma *et al.*, 2019).

Four trophic groups based on morphology and gut content analysis have been distinguished, following the humification gradient ranging from intact wood to soil organic matter (Donovan *et al.*, 2001). Wood- or grass-feeding termites (Group I) are the only guild of 'lower termites' with symbiotic protists in their gut. This group includes termites of the families Rhinotermitidae and Kalotermitidae, which feed on young dead wood, and grass-feeding termites mainly of the family Hodotermitidae to which the European termites such as *Reticulitermes* spp. belong. 'Higher termites' (Termitidae) can be classified into three groups. Litter-, dead wood-, grass-feeding termites (Group II) is a heterogeneous group of termites that feed on plant materials with a low level of humification. In comparison to Group I, leaf-litter-feeding is ecologically much more important within this group. All Macrotermitinae and a subgroup of micro-epiphyte-feeding termites, for example *Hospitalitermes* and *Longipeditermes*, are in this group. Upper-soil-layer-feeding termites (Group III) feed on organic matter-rich substrates in the litter–soil interface, with litter and wood in an advanced stage of decay the primary food source of this group. All Foraminitermitinae termites belong to this group. True soil-feeding termites (Group IV) form a derived group of termites feeding on soil containing various amounts of mineral material, but always rich in highly humified organic matter. A typical genus represented only within this group is *Cubitermes*, which builds mushroom-like soil nests in the humid tropics. Species of various termite genera, such as *Anoplotermes*, *Amitermes*, *Termes*, *Cornitermes* and *Nasutitermes*, may belong to more than one feeding group.

Studying the feeding habits of termites is especially informative when colonies of a given species, or more importantly colonies in different regions or continents are compared. This allows better assignment of the predominant food source to a certain species while accounting for variability arising from geographical or habitat differences. Combining the most promising methods, that is field observations and stable isotope analyses may allow accurate identification of trophic position. Stable isotope analyses of N and C revealed the position of the main food source of termites within the humification gradient (Hyodo *et al.*, 2008, 2011). Trophic niche differentiation among closely related termite species at one site was revealed by strong deviations in stable isotope ratios (Bourguignon *et al.*, 2009; Schyra, Scheu & Korb, 2018), providing a partial explanation for how multiple related species of termites can co-exist at one site. Radiocarbon (^{14}C) analysis was used to estimate the mean age of the termite diet in two tropical regions, confirming that grass-feeding termites consume the youngest diet (2 years old), followed by leaf-litter feeders (5–9 years old), while soil and wood-feeders consume older organic matter (up to 50 years) (Hyodo, Tayasu & Wada, 2006; Hyodo *et al.*, 2008). Analysis of carbon isotope composition of nestmates within a single *Macrotermes* colony showed that while the queen and larvae consumed fungal mycelium, workers and soldiers consumed plant and fungus comb material (Vesala, Arppe & Rikkinen, 2019). Additionally, a distinctive difference in fatty acid composition of termite bodies was used to indicate the degree of wood decay of the substrates these termites feed on preferentially (Carter, Dinus & Smythe, 1972), although fatty acid composition may vary among termite developmental stages (Chen & Laine, 2016). These novel methods could be especially powerful in combination with visual gut content analysis (Donovan *et al.*, 2001; Janei *et al.*, 2020). Extensive research has focused on the production and activity of digestive enzymes such as xylanases, cellulases and lignin-modifying enzymes of termites and, more importantly, those of their gut symbionts (Ni & Tokuda, 2013; Brune, 2014).

Advances in species identification and use of various diet-tracing methods is a necessity to understand how whole termite communities fit into the detrital soil food web. Another issue is the unknown efficiency of termites in decomposing dead plant material in comparison to other soil biota, that is other arthropods or microbes. Exclusion experiments (Ashton *et al.*, 2019) restricting termites from a site or their utilisation of experimentally added and/or protected food particles could provide useful information. Finally, the importance of termites as prey is poorly understood. Since termites show high abundances and can support populations of a variety of predators, they may shape the entire detrital food web in some ecosystems.

(*k*) *Thysanoptera*

Key message: *thrips are small-sized insects, feeding on living plant material and fungi. The group can be divided into fungal feeders (majority of Tubulifera) and plant feeders (majority of Terebrantia).*

Thysanoptera (thrips) are globally distributed in grasslands, forests and even deserts (Lewis, 1973). Overall, about 6300 species in two suborders, Terebrantia (~2500) and Tubulifera (~3700) are described (ThripsWiki, 2021) with the highest diversity in the tropics (Alves-Silva & Del-Claro, 2010). Thysanoptera exhibit diverse feeding habits with most species feeding on plants or fungi using their asymmetric piercing–sucking mouthparts (Chisholm & Lewis, 1984). However, few species consume mosses, ferns, lichens or arthropods, form galls, or live as ectoparasites (Mound & Marullo, 1996; Izzo, Agbowo & Bruns, 2005).

Fungal feeding mainly occurs within the suborder Tubulifera in approximately 60% of species. Species of the subfamily Phlaeothripinae suck on fungal hyphae in the soil and litter layer as well as on dead twigs and leaves, while species of the subfamily Idolothripinae consume fungal spores (Mound, 2001). In the suborder Terebrantia, a minor proportion of species feed on fungal hyphae, restricted to the families Merothripidae and Uzelothripidae (Lewis, 1973; Mound & Teulon, 1995; Mound, 2005). The large majority of the Terebrantia (including the most species-rich family Thripidae) predominantly feed on various plant parts including leaves, pollen and flower tissue. These may be pest species that act as vectors for plant pathogens causing severe losses in crop production. Phytophagous Thysanoptera are connected to the belowground system by overwintering in soil or the litter layer of their host plant or by remaining in the soil during certain stages of larval development (Cho *et al.*, 1995; Moritz, 1997).

While predacious mites, parasitic nematodes and anthocorid bugs are known to reduce thrip populations, at least for a few well-investigated pest species in agricultural fields, information on potential predators under natural conditions is lacking for most non-pest species (Sabelis & Rijn, 1997; Mound, 2005). Similarly, with the exception of few pest species, feeding behaviour of most phytophagous as well as fungi associated thrips species is unknown (Kirk, 1995; Mound & Teulon, 1995; Mound, 2005, 2014). Studies on the litter fauna have largely failed to investigate Thysanoptera (Mound, 2014). A future goal should be to have a closer look at the biology of tropical thrip species associated with detritus and fungi.

(*l*) *Hemiptera*

Key message: *Hemiptera have piercing–sucking mouthparts and most live as herbivores, except for some predatory Heteroptera families.*

With more than 100,000 species, Hemiptera is an omnipresent order of insects that includes the following major groups (Cranston & Gullan, 2009; Cryan & Urban, 2011; Zhang, 2011): Sternorrhyncha (scale insects, aphids, whiteflies, etc.), Auchenorrhyncha (e.g. cicadas, leafhoppers), Coleorrhyncha (moss bugs) and Heteroptera (true bugs *sensu stricto*). All Hemiptera have piercing–sucking mouthparts and the first three groups feed almost exclusively by sucking plant sap from shoots or roots. Feeding habits of Heteroptera range from phytophagy to predation, including ectoparasitism and haematophagy. Phytophagous Hemiptera cause major damage to agricultural crops worldwide by direct feeding and transmission of geminiviruses (Kaloshian & Walling, 2005; Jackson *et al.*, 2012; Sarmad *et al.*, 2020) and indirectly impact soil food webs *via* plant nutrition (Wardle *et al.*, 2004; Grabmaier *et al.*, 2014). Studies based on stable isotope analysis revealed that phytophagous Hemiptera are closely associated with primary production, which is useful for assessing partitioning of resources and food-web reconstruction (Okuzaki *et al.*, 2010; Wilson, Sternberg & Hurley, 2011; Jackson *et al.*, 2012; Lagerlöf *et al.*, 2017).

Various species of phytophagous Hemiptera including Auchenorrhyncha and Sternorrhyncha are associated with plant roots. To protect themselves, many of them form a mutualistic relationship with ants known as 'trophobiosis', in which the ants consume excreted honeydew (Delabie, 2001). A well-known example of this association in soil is species of the ant genus *Lasius* that tend various root aphid species (Depa & Wojciechowski, 2008). Among other belowground Hemiptera, the juvenile stages of cicadas (Auchenorrhyncha) feed on the roots of plants, for periods as long as 13 or 17 years for some taxa (e.g. *Magicicada* spp.). The emergence of adults represents a significant movement of energy and nutrients (such as N) from belowground to aboveground pools (Callaham Jr *et al.*, 2000; Whiles *et al.*, 2001), where they support various predators (e.g. spiders, mantids) and parasitic insects.

Plant-feeding species also make up the majority of Heteroptera, but predators are found in most families (Sanderson, 1992; Schuh & Slater, 1995). Heteroptera include both obligate phytophages (e.g. Tingidae and Coreidae) and obligate predators (e.g. Reduviidae, Phymatidae and Nabidae). Predatory Heteroptera can also feed on plants, but cannot survive on plants alone (Torres & Boyd, 2009). Primarily phytophagous species (e.g. *Lygus hesperus* and *L. lineolaris*) possess salivary pectinases and amylases that are indicative of herbivory, but also in some cases have venoms and phospholipases, distinctive of specialised carnivores, suggesting the presence of omnivory even in herbivorous Heteroptera (Coll & Guershon, 2002). Important morphological traits which may help to classify Heteroptera into trophic groups include mouthpart morphology. In general, mandibular stylets of predatory Heteroptera are curved and armed with hook-like teeth, which enable them to grasp their prey. By contrast, stylets of phytophagous Heteroptera are usually straight and possess teeth which are curved towards the plant surface or may have no teeth at all. The stylets of omnivorous species lack notable teeth (Coll & Guershon, 2002). All these groups are often found on the ground and interact with other soil-associated invertebrates.

Overall, most Hemiptera can be assigned as phytophages in soil food webs with the exception of some predatory Heteroptera. Future studies could focus on revealing gaps in existing data on Hemiptera as an important indirect agent in belowground–aboveground interactions.

(*m*) *Psocoptera*

Key message: *booklice are microbivores, but their food preferences are poorly known.*

Psocoptera (booklice, psocids) contain about 6000 described species with the highest species richness in the tropics (Anonby, 2019), but they also are regularly found in the litter of temperate forests (Thornton, 1985). However, usually they make up only a small proportion of soil arthropods (Baz, 1991). Psocoptera have chewing mandibles and act as microbivores, feeding on algae, lichens, fungal mycelia and occasionally on pollen grains (Lienhard, 1998; Anonby, 2019). Psocoptera are prey for many invertebrate species including spiders, assassin bugs and ants (Requena, Buzatto & Machado, 2007). Living in groups and camouflage represent their main defence mechanisms against predators (New & Collins, 1987). Psocoptera are divided into ecological groups by their vertical stratification, which is related to their association with soil food webs and food: primary (true) litter dwellers, secondary litter dwellers (one generation in litter and others elsewhere) and occasional litter dwellers (New & Collins, 1987; Baz, 1991). Psocoptera is among the least-studied groups of soil-associated insects with their functional roles remaining unclear. Most studies on Psocoptera focus on taxonomy or the biology of species of economic importance (Requena *et al.*, 2007). At present, litter-dwelling Psocoptera may best be classified as microbivores.

(*n*) *Formicidae and other Hymenoptera*

Key message: *ants include predators, scavengers, herbivores and granivores. Without knowledge of the species composition, ants as a group are often classified as omnivores. Most soil-dwelling and soil-foraging ants depend on protein-rich food resources and predominantly live as predators.*

Formicidae (ants) are an abundant, widespread and diverse group of eusocial insects and the main hymenopterans in soil. There are about 16,000 ant species and their biomass may represent up to 20–50% of the total arthropod biomass in tropical and subtropical communities (Dial *et al.*, 2006; Tuma *et al.*, 2020). Ants may increase plant growth by preying on insect herbivores (Schmitz, Hambäck & Beckerman, 2017). They occupy most ecosystem strata including trees, litter and soil, either for nesting or foraging, with many species connecting different ecosystem compartments. Ants are important predators, scavengers, direct or indirect herbivores, seed dispersers and soil bioturbators. By their nest-building activities and food accumulation, ants affect nutrient distribution and availability, thereby affecting plant growth (Frouz & Jílková, 2008; Evans *et al.*, 2011). Ants are involved in numerous interactions with plants, fungi and other arthropods. By predation, mutualistic interactions or niche provisioning (providing microhabitats in ant soil nests) they can shape whole communities of soil microbiota and arthropods (Laakso & Setälä, 1998; Floren, Biun & Linsenmair, 2002; Boulton, Jaffee & Scow, 2003).

Ants are traditionally defined as omnivores feeding opportunistically on a wide spectrum of resources (Stradling, 1978; Hölldobler & Wilson, 1990; King, 2016). They explore the environment individually, but communicate using pheromones and recruit companions, giving them a competitive advantage in foraging for dispersed resources. They are also capable of overcoming and carrying large animal prey or carrion by cooperative action. Ants' diet include earthworms, termites, caterpillars, springtails, flies, aphids, spiders and other invertebrates of different developmental stages, and even small vertebrates such as frogs or lizards. Ants can be responsible for 61% of arthropod-removed food items of various origin on the rainforest floor (Griffiths *et al.*, 2018). Ants are preyed upon by a wide spectrum of animals including vertebrates, such as anteaters, aardvarks, pangolins, birds, frogs and lizards, as well as other arthropods such as ant-preying ants (especially army ants), antlions, assassin bugs, specialised spiders, beetles and by mites that prey on their brood (Bequaert, 1922). All these predators affect ant populations, however, there is no comprehensive and quantitative review on this topic.

The main trophic guilds of ants are based on the food resources they predominantly use. Most ant species are omnivores feeding on a variety of sugar- and protein-rich diets with little or no clear preferences. General predators and scavengers prey or collect a diversity of protein-rich resources such as dead insects. Specialised predators are less common among ants. They include predators of termites (e.g. *Megaponera analis*) (Bayliss & Fielding, 2002), other ants (e.g. *Nomamyrmex esenbeckii*) (Souza & Moura, 2008), springtails for trap-jaw ants with fast snapping mandibles (e.g. *Strumigenys*) (Brown, 1962), and of rarer prey groups such as polyxenids for the specialised ant predator *Thaumatomyrmex paludis* (Rabeling, Verhaagh & Garcia, 2012) or spider eggs for the small ants *Proceratium* spp. (Brown, 1979) and *Discothyrea* spp. (Dejean & Dejean, 1998). There is evidence that small ants of the genus *Pheidole* prefer to feed on oribatid mites, despite the mites' strong cuticle protecting them against predators (Wilson, 2005).

Mediated herbivores (indirect herbivores) are a large group of ants that feed on plant-derived resources. Generally, the role of ants as herbivores has been underestimated (Tobin, 1994) and is likely of importance for the energy flux in many ecosystems (Davidson *et al.*, 2003). Fungus-gardening tropical ants (mainly *Attini* leaf-cutting ants and their fungal partner *Leucocoprinus*) use their mutualistic fungal partners to transform nutrients from plant leaves into digestible food (Boulogne, Ozier-Lafontaine & Loranger-Merciris, 2014). Granivores, including *Pogonomyrmex*, *Pheidole*, *Solenopsis*, *Tetramorium* and *Aphaenogaster*, collect a variety of plant seeds and process them into a fermented mixture for consumption. These ants also perform a significant ecosystem service as seed-dispersers, as not all seeds are successfully transported into the nest and eaten (Lengyel *et al.*, 2009). This group is important predominantly in dry regions such as most of the Mediterranean, where for example *Messor* spp. ants often dominate and harvest a large proportion of seeds (Díaz, 2016). Some ants form mutualistic relationships with sap-sucking insects (trophobiosis), such as aphids (Aphidina) or scale insects (Coccidea), and eat their sugar-rich excreta (honeydew). Apart from ants tending their mutualistic partners aboveground in the canopy or on low vegetation, some species tend sap-sucking insects on the roots of plants in soil (Styrsky & Eubanks, 2007).

Overall, ants may be considered omnivores, especially when their species composition is not known or there is little information on their life history. However, if species are identified and their feeding habits known, the predominant food resources of these ants can be identified, allowing us to ascribe their position in food webs more precisely. Typical soil-dwelling and soil-foraging ants (Ponerinae, Dorylinae and Amblyoponinae) may predominantly live as predators depending on protein-rich rather than sugar-based resources (Jeanne, 1979; Cerdá & Dejean, 2011). On the other hand, species like *Lasius flavus* in temperate regions or *Acropyga* spp. in the tropics, which barely leave the soil, tend hemipterans directly on plant roots and sugar represents their main food resource (Agosti, Majer & Alonso, 2000). Thus, species identification and assigning individual species to trophic guilds rather than grouping them into a general group such as 'predators' or 'omnivores' is desirable. This can be achieved using either published feeding guild summaries for a locality [e.g. Silvestre, Brandao & Paiva, 2017 for part of Brazil] or more general summaries (Lanan, 2014) or species accounts at AntWiki (2020) and references therein.

The above-mentioned trophic guilds are not exclusive and different ant species may modify their nutrition according to season. The worker caste of the majority of ant species depends largely on sugars, but the larvae feed mainly on protein-rich material. As the number of larvae in a colony fluctuates during the season, the target food source is likely to change accordingly (Portha, 2002; King, 2016). Conversely, even ant species that are considered to be predators (e.g. *Aenictus* spp. or *Leptogenys* spp.) may accept sugar-rich fluids when available (Hashimoto, Yamane & Itoka, 1997). The feeding strategies of soil-dwelling ants are especially understudied. Stable isotope analysis has revealed the trophic relationships between predators and sap-collecting species (Blüthgen, Gebauer & Fiedler, 2003) and showed the importance of other food sources for honeydew-feeding ants in plantations (Brewitt *et al.*, 2015). A combination of fatty acid analysis, baiting and stable isotope analysis of temperate and tropical ant communities confirmed that ants are generalists with a few, mainly tropical, species preferring a particular food resource (Rosumek *et al.*, 2018). Additionally, ant trophic assemblages appear to be conserved across the habitat modification gradient, but shifts towards herbivory may occur in areas with more herbivorous arthropods due to honeydew availability (Gibb & Cunningham, 2011). DNA barcoding of ant gut contents allowed the identification of their prey: 17% of 15 species of tropical ants investigated had termite DNA in their guts (Fayle *et al.*, 2015) and it appears that predation rates do not differ between natural habitats and plantations (J. Tuma, S.H. Luke, R.G. Davies, P. Eggleton, P. Klimes, D.T. Jones, H. Konvickova, P.M. Maraví, S.T. Segar & T.M. Fayle, unpublished data). Unfortunately, almost none of the existing methods can distinguish unambiguously between predation and scavenging; opportunistic scavenging may be common in predatory ants (Tschinkel, 2006). However, it is an important distinction as it defines their actual role in ecosystem processes and food webs. Isoenzyme electrophoresis may allow differentiating between active predation and scavenging, but has been little used to date (Juen & Traugott, 2005). Another limitation is of a rather semantic nature. We consider soil-nesting ants to be part of the soil fauna, thus participating in soil food webs. Nevertheless, many ants nest in soil but most of their activities (i.e. foraging) take place in higher strata, from the litter and herb layer to the canopy of trees. Thus, their role in soil food webs *senso stricto* is open to question. The faeces and the nutrients therein commonly are deposited and released within the soil nest, but the role of such ants as predators of other soil fauna is probably small (Lenoir, Bengtsson & Persson, 2003). Nevertheless, their presence facilitates the presence of myrmecophilous soil fauna (Boulton & Amberman, 2006) and this role should be further investigated.

In addition to ants, many solitary bees and most solitary wasps in the superfamily Vespoidea and some of the social wasps (e.g. *Vespula*) construct nests in soil or on the soil surface (Coleman *et al.*, 2017). Stable isotope analyses suggest that the feeding habits of these wasps range from omnivory with some dependence on nectar and honeydew to intraguild predation (Chikaraishi *et al.*, 2011; Hyodo *et al.*, 2011). Adult insects may have an important role in soil food webs due to predation on various invertebrates, including other predators (e.g. spider-hunting wasps Pompilidae, Sphecidae, Crabronidae) (Hastings *et al.*, 2010). In turn, soil-developing larvae may serve as food for soil predators.

(*o*) *Coleoptera*

Key message: beetles are a keystone group (together with Diptera) that integrate energy across belowground and aboveground invertebrate communities. At least family-level identification is necessary to assign Coleoptera to trophic guilds such as predators (e.g. Carabidae, Staphylinidae, Cantharidae), omnivores (e.g. Elateridae), and saprophages/root feeders (e.g. Scarabaeidae, Curculionidae). However, many families of Coleoptera contain predatory, herbivorous and fungivorous species.

Coleoptera (beetles) is the most species-rich order of animals with about 400,000 described species (Bouchard *et al.*, 2017). Beetles occupy an extremely high diversity of ecological niches and thus may affect most ecosystem functions. In terrestrial ecosystems, beetles feed on plants (e.g. Curculionidae, Chrysomelidae), litter (e.g. some Scarabaeidae, Tenebrionidae), fungal tissues (e.g. Mycetophagidae, Staphylinidae: Oxyporinae), soil invertebrates (e.g. Carabidae, Cantharidae), corpses and dung of vertebrates (e.g. Silphidae, Geotrupidae, Nitidulidae), and dry wood (Cerambycidae, Anobiidae) as well as other substrates (Marshall, 2018). Beetles themselves serve as prey for a number of species of large predatory arthropods (Polis, 1979), amphibians (Ruchin & Ryzhov, 2002; Balint *et al.*, 2008), birds (Riegert & Fuchs, 2004; Romanowski, Altenburg & Zmihorski, 2013) and mammals (Fisher & Dickman, 1993; Colon & Sugau, 2012). As adults, many species of beetles are protected against predation by poison or sclerotised cuticles. Less-protected larvae, however, live in hidden microhabitats (Marshall, 2018). Almost all Coleoptera species have at least one stage (egg, larva, pupa or imago) in soil or litter and may be considered part of detrital food webs (Ghilarov, 1949). Among the 211 families of Coleoptera (Bouchard *et al.*, 2011), the following are most abundant in soil food webs: Carabidae, Staphylinidae, Cantharidae, Curculionidae, Elateridae and Scarabaeidae.

Most Carabidae (ground beetles) are considered generalist predators consuming a wide range of animal prey, but also occasionally feed on plant material (Soboleva-Dokuchaeva, 1975; Thiele, 1977; Lindroth, 1992). The other two important trophic guilds of ground beetles comprise polyphagous phytophages (most belonging to the tribes Harpalini and Zabrini) and myrmecophilous forms (tribe Paussini) inhabiting colonies of ants (Sharova, 1981). Medium and large ground beetles predominantly feed on larger prey and rarely on microarthropods (Federmann, 1983). However, some more specialised groups are known to feed on springtails (*Loricera* and *Notiophilus*; Bauer, 1979; Bauer, 1986) or molluscs (*Cychrus*; Tod, 1973). DNA-based molecular gut content analysis showed the importance of springtails and earthworms in the diet of Carabidae larvae in arable ecosystems (Eitzinger & Traugott, 2011). High levels of intraguild predation among ground beetles were revealed using molecular techniques in winter wheat fields (Davey *et al.*, 2013). Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), confirmed earlier trophic classification of polyphagous species of ground beetles (Sasakawa, Ikeda & Kubota, 2010; Kamenova *et al.*, 2018). The method also revealed high inter-site variability in trophic niches of ground beetles (Zalewski *et al.*, 2016) and sex-related differences in resource allocation (Goncharov *et al.*, 2015). However, neither DNA-based techniques nor stable isotope methods were able to explain the high alpha-diversity of ground beetles (up to 45 species per experimental site) in terrestrial ecosystems (Okuzaki *et al.*, 2009; Kamenova *et al.*, 2018). Besides differences in seasonal and daily activity, migration may be an important mechanism driving partitioning of trophic niches in communities of polyphagous ground beetles (Matalin & Makarov, 2011; Zalewski *et al.*, 2015). Using stable isotope ratios of hydrogen (δD) and oxygen ($\delta^{18}O$) has allowed tracing of long-range migrations of ground beetles (Palmu *et al.*, 2017), making this a promising approach for evaluating the spatial niche differentiation and spatial heterogeneity of detrital food webs.

The great majority of Staphylinidae (rove beetles) are predators (Thayer, 2005). However, associations with fungi have been of particular importance during their evolution and have contributed significantly to the enormous diversification of this group (Newton, 1984). Shifts in feeding preference are known not only between tribes and genera, but even within the same genus of Staphylinidae (Leschen, 1993). In ephemeral substrates (manure, fruiting bodies of mushrooms, corpses, etc.), rove beetles often represent the main group of macrofauna predators (Tikhomirova, 1982). Based on traditional methods, omaliine rove beetles have been classified as predators, saprophages and (at least facultatively) mycophages; tachyporine rove beetles consist of both predators (Tachyporinae and Trichophyinae) and fungi feeders (Habrocerinae and Aleocharinae); oxyteline rove beetles are represented by mycophages, saprophages and species with unclear feeding habits; staphylinine rove beetles are either mycophages (Oxyporinae) or predators (Pseudopsinae and Megalopsidiinae) (Tikhomirova, 1973; Ashe, 1984; Lipkow & Betz, 2005). Molecular gut content analysis provided information on the fungal community composition in the gut of nine abundant rove beetle species from boreal forest (Stefani *et al.*, 2016). Stable isotope techniques confirmed a high level of diversification of trophic niches among rove beetles (Scheu & Falca, 2000; Illig *et al.*, 2005; Oelbermann & Scheu, 2010). Our understanding of the feeding ecology of Staphylinidae is hampered in part by difficult species identification and progress is expected by combining novel methods in trophic ecology and taxonomic advances. In general, the group can be reasonably classified as predators with some mycophagy.

The larvae of most species of Cantharidae, Curculionidae, Elateridae and Scarabaeidae live in soil. A number of species from these groups are important pests (Curculionidae, Elateridae, and Scarabaeidae) or biocontrol agents (Cantharidae) (Marshall, 2018). DNA-based techniques allowed specification of the efficient natural enemies of pest species of Curculionidae (Schmidt, Szendrei & Grieshop, 2016a), Chrysomelidae (Lundgren, Ellsbury & Prischmann, 2009; Kheirodin *et al.*, 2020) and Scarabaeidae (Juen & Traugott, 2007).

Based on traditional methods, Cantharidae larvae have been considered predators in temperate ecosystems (Leschen, Beutel & Lawrence, 2010). Stable isotope labelling showed that Cantharidae are linked to freshly fixed plant carbon, likely *via* predation on root-associated invertebrates (Goncharov *et al.*, 2016). Molecular gut content analysis documented the importance of springtails and earthworms as part of the diet of Cantharidae larvae in arable ecosystems (Eitzinger & Traugott, 2011).

Despite morphological similarity within the group, Elateridae (wireworms) demonstrate a wide range of different feeding habits including phytophagy, saprophagy, predation, necrophagy and coprophagy (Dobrovolsky, 1970). Thus, many species of this family can be classified as omnivores.

Stable isotope analysis showed that wireworms have a complex feeding behaviour at the individual level and a number of wireworm species are able to switch from saprophagy to predation during dryer conditions (Traugott *et al.*, 2008; Samoylova & Tiunov, 2017). Natural differences in δ^{13}C signatures between C3 plants (wheat and grasses) and C4 plants (maize) have been used to determine the activity of Elateridae adults (Schallhart *et al.*, 2009) and larvae (Schallhart *et al.*, 2011).

Soil-dwelling larvae of Scarabaeidae can feed on living roots of various species and on a wide range of soil organic substrates (Marshall, 2018). Stable isotope analysis confirmed earlier suggestions that many Scarabaeidae larvae live as saprophages (Kupfer *et al.*, 2006; Hyodo *et al.*, 2010b; Tsurikov, Goncharov & Tiunov, 2015). Fatty acid analysis further showed that omnivorous soil-dwelling larvae of Scarabaeidae feed on soil organic matter rather than plant roots or wood flakes (Tsunoda, Suzuki & Kaneko, 2017). Molecular gut content analysis showed that root-feeding larvae of *Phyllopertha horticola* (Scarabaeidae) serve as an important food source for some predatory Carabidae larvae as well as Geophilidae and Lithobiidae (Juen & Traugott, 2007).

Many larvae of Curculionidae species feed on roots and are considered pests closely connected to soil food webs (Jenkins *et al.*, 2006). Unlike Scarabaeidae, among which both phytophagous and saprophagous soil-living larvae are known, most soil Curculionidae feed exclusively on living plant roots (Marshall, 2018). DNA-based techniques showed that natural enemies of pest species of Curculionidae include predatory bugs (Nabidae and Pentatomidae), spiders and beetles (Schmidt *et al.*, 2016a).

Due to their relatively large size, economic importance and pronounced morphological features closely related to the ecological niche occupied, key feeding habits of common Coleoptera species and groups of species were described in the 20th century using traditional methods. Application of molecular gut content, fatty acid and stable isotope analyses allowed clarification and unravelling of the mechanisms driving intra- and interspecific interactions of Coleoptera at high taxonomic resolution. Investigations of feeding habits of Coleoptera are complicated primarily by the high species diversity of this group and the fact that only for a small proportion of species is information on the morphology, physiology and ontogenesis available.

(*p*) *Lepidoptera*

Key message: soil-dwelling butterfly larvae are mainly herbivorous, but the importance of alternative food resources needs to be assessed.

Lepidoptera (butterflies) are one of the most diverse phytophagous insect groups with approximately 160,000 species worldwide (Pogue, 2009; Wahlberg, Wheat & Peña, 2013). The majority of Lepidoptera larvae (caterpillars) feed on aboveground plant parts (Powell, Mitter & Farrell, 1998) and outbreaks can lead to pronounced cascading impacts on the soil food web (Frost & Hunter, 2008; Kaukonen *et al.*, 2013). In soil, Lepidoptera are only present as larvae and pupae (e.g. Brahmaeidae, Geometridae, Lymantriidae, Noctuidae, Pyralidae, Sphingidae), but typically only at low densities (Adams *et al.*, 2016), not exceeding 0.5–5.0% of total soil macrofauna abundance (Gongalsky, Pokarzhevskii & Savin, 2006; Brévault *et al.*, 2007; Korobushkin *et al.*, 2019; De Vasconcelos *et al.*, 2020). However, root-eating caterpillars can consume up to 7.5% of annual root production (Krivolutsky *et al.*, 1985). Caterpillars themselves are prey for various soil predators. Many species of Lycaenidae, Riodinidae and Tortricidae form obligate or facultative symbiosis with ants, ranging from mutualism to parasitism (Pierce *et al.*, 2002). Caterpillars are collectively perceived as herbivorous, but in fact they span a wide range of trophic guilds from herbivores to detritivores, lichen and fungal feeders, and even predators (Pierce, 1995; Powell *et al.*, 1998; Adams *et al.*, 2016). Often, species switch or mix diets to support nutritional balance, or feed opportunistically exploiting different food sources (Singer & Stireman, 2001; Bodner, Brehm & Fiedler, 2015). However, studies based on stable isotope analysis showed that common soil Lepidoptera species (mostly Geometridae and Noctuidae) mainly act as primary consumers feeding on live plant tissue (Okuzaki *et al.*, 2009, 2010; Ikeda *et al.*, 2010) but some species may additionally consume detritus and saprotrophic fungi (Okuzaki *et al.*, 2009, 2010; Ikeda *et al.*, 2010). Overall, without further research, soil-dwelling Lepidoptera can be classified as herbivores.

(*q*) *Diptera*

Key message: fly larvae are difficult to classify in soil food webs as their feeding habits vary from detritivory to fungivory to predation. Identification at least to suborder or family level is needed to ascribe them to trophic groups, but some taxa are trophically diverse despite being morphologically similar. As a group, they can be classified only as omnivores.

Diptera, or true flies, comprise *ca.* 160,000 species, and are one of the most ecologically diverse orders of insects, spanning ecological roles from detritivory and herbivory to predation (Yeates *et al.*, 2007). Most Diptera taxa spend their larval stages in soil, but a few groups live in the soil throughout their life cycle (e.g. wingless Sciaridae and Cecidomyiidae). Soil-dwelling Diptera larvae are an important, often dominant, part of soil macrofauna in a wide range of ecosystems – from forests to agroecosystems (Frouz, 1999; Seeber *et al.*, 2005). Dipteran larvae are prey for many predatory macroinvertebrates including centipedes, carabid beetles, harvestmen and spiders, as well as other Diptera.

Diptera are trophically very diverse and occupy all trophic levels in soil food webs. Stable isotope analyses confirmed the wide variety of trophic positions occupied by soil Diptera larvae. On average they are enriched in ^{13}C, suggesting that most rely on microorganisms or microbially processed organic matter as basal resources (Potapov *et al.*, 2019b). Isotopic labelling experiments, however, showed that some species of Diptera larvae (Bibionidae and Sciaridae) consume freshly fixed carbon *via* feeding on live roots or mycorrhizal fungi (Goncharov *et al.*, 2016). Soil-associated Diptera larvae have been divided into several functional groups (Hovemeyer, 1984; Frouz, 1999), which are mainly confirmed by stable isotope analyses (Seeber *et al.*, 2005; Okuzaki *et al.*, 2009; Korobushkin *et al.*, 2014; Goncharov & Tiunov, 2014; Zuev *et al.*, 2019). These include: (*i*) saprophages and phytosaprophages consuming large particles of dead or living plant material (e.g. Trichoceridae, Tipulidae, some Limoniidae, Bibionidae, some Sciaridae, Scatopsidae); (*ii*) surface scrapers consuming fine particles from the surface of the litter including algae and fungi, protozoa, nematodes and amorphous detritus (e.g. Lonchopteridae, Phoridae, Drosophilidae, Otiitidae, Lauxanidae, Fannidae); (*iii*) microphages consuming fine particles in the soil including algae, fungi, moss and microfauna (e.g. Chironomidae, Ceratopogonidae, Stratiomyidae); (*iv*) mycophages selectively feeding on hyphae of fungi (e.g. Cecidomyiidae, Anthomyiidae, Mycetophilidae); (*v*) predators feeding on soil oligochaetes, other soil insects (particularly larvae) including other Diptera (e.g. Empidoidea, Tabanidae, Rhagionidae, Therevidae, some Muscidae). Morphologically most saprophagous and fungivorous dipterans belong to Nematocera (Hennig, 1973), the larvae of which mainly develop in soil, litter and wood. Many Brachycera are predators; however, there also are a range of saprophagous taxa (e.g. Stratiomyidae, Xylophagidae, Lonchopteridae, Phoridae, Syrphidae) (Borin & Herlitzius, 1987; Frouz *et al.*, 2002). An informative trait to predict the trophic position of some families (e.g. Syrphidae, Muscidae) is the thorax form of the larvae (Rotheray & Wilkinson, 2015). In contrast to phytophagous and saprophagous species, the thorax of predatory Muscomorpha larvae tapers towards the front, facilitating penetration into the prey body.

Diptera play a keystone role in cross-habitat linkages through the transfer of matter and energy, which is very important at the boundaries of aquatic–terrestrial ecosystems (Hoekman *et al.*, 2011; Lafage *et al.*, 2019). Studies based on stable isotope (Collier, Bury & Gibbs, 2002; Sanzone *et al.*, 2003; Paetzold, Bernet & Tockner, 2006; Mellbrand *et al.*, 2011) and fatty acid analyses (Gladyshev, Arts & Sushchik, 2009; Gladyshev, Gladysheva & Sushchik, 2019; Moyo, 2020) showed that adult Diptera emergent from water can be an important or even the main source supporting the high density and diversity of invertebrates in adjacent terrestrial ecosystems (Gratton, Donaldson & Zanden, 2008; Korobushkin *et al.*, 2016; Radermacher *et al.*, 2020). Overall, Diptera are trophically diverse even though they may be morphologically similar. As a group, they can be classified only as omnivores. Identification at least to suborder or family is necessary to ascribe them to more specific trophic groups. Considering the trophic diversity of Diptera, future studies need to integrate traits and novel methods for tracing trophic niches to allow a deeper understanding of this important component of belowground food webs.

(4) Other invertebrates

(*a*) *Lumbricina*

Key message: earthworms feed on either plant residues (litter and rotten wood) or soil organic matter. Soil-feeding species ingest and digest whole soil ecosystem compartments, and their functions as ecosystem engineers arise from this prodigious feeding.

As is reflected in their common name in many languages, earthworms (Lumbricina) are probably the most widely recognised invertebrates that dwell in 'earth', are born and die in earth, and even eat earth as their main food. They represent and embody a true soil animal in all respects of common understanding; they are ubiquitous and their beneficial roles in soils are also widely appreciated. About 7000 earthworm species have been described to date (Orgiazzi *et al.*, 2016). And yet, our knowledge on how they meet their food requirements is limited. As was discussed in Section I.2, earthworms are usually classified according to morphology and behaviour into three ecological groups: epigeic, anecic and endogeic. However, considering their food source alone, we know from direct observation that earthworms eat either mineral soil or plant residues such as leaf litter (Satchell, 1967).

The first group, mineral soil feeders, are typified by the endogeic species, however, anecics also ingest soil for burrow construction and maintenance. Since mineral soil is of low nutritional quality, it is ingested and egested in large quantities, in extreme cases several times the body mass of an individual per day (Curry & Schmidt, 2007). This results in earthworms functioning as 'ecosystem engineers' (Blouin *et al.*, 2013) based on soil bioturbation, aggregate formation, macropore construction, and mixing of mineral and organic materials. Food choice experiments showed that soil-feeding earthworms prefer soil patches that are rich in organic matter and microorganisms (Hendriksen, 1991; Bonkowski & Schaefer, 1997), but they always require mineral (sand) grains as part of their diet (Doube *et al.*, 1997), which probably reflects a physical function in digestion (Schulmann & Tiunov, 1999). Microscopic gut content analyses have identified a wide range of ingested materials and organisms, including plant and leaf fragments, charcoal, seeds, pollen, algae, fungi, nematodes, protozoa and amorphous organic matter, always mixed with a soil mineral matrix (Bouche & Kretzschmar, 1974; Piearce, 1978; James & Cunningham, 1989; Bernier, 1998). This seemingly indiscriminate ingestion by these large soil invertebrates led Pokarzhevskii *et al.* (1997) to call them "ecosystemivorous", that is earthworms swallow entire soil ecosystems and therefore presumably occupy a unique position in the food web.

The second group of earthworms, that is those that feed on plant residues, includes the epigeics, which typically live in their food substrate, and the anecics, that forage at the soil surface and drag food items into their channels. These earthworms feed on all kinds of dead plant materials, but in general they prefer more palatable, nutrient-rich materials (low C:N ratio) that are low in plant secondary compounds and colonised by decomposing microbes (Wright, 1972; Hendriksen, 1990; Schonholzer *et al.*, 1998; Curry & Schmidt, 2007). Dung of ungulates (i.e. processed plant materials) is also highly attractive to these earthworms (Bacher *et al.*, 2018). Growth experiments suggest that nutrients from plant matter (or dung) are digested directly (Hendriksen, 1991; Ashwood *et al.*, 2017) but earthworms also consume and digest microorganisms, in particular, fungi (Maraun *et al.*, 2003; Salamon *et al.*, 2006).

Herbivory on living plants or seedlings has also been observed (Griffith *et al.*, 2013; Kirchberger *et al.*, 2015), but is probably incidental since some litter-feeding, surface-foraging earthworm species drag all kinds of plant materials and objects into their burrows. The reported digestion of living plant seeds during gut passage (Eisenhauer, Marhan & Scheu, 2008), however, documents that earthworms also function as herbivores and can affect plant recruitment (Milcu, Schumacher & Scheu, 2006). Much less is known about the role of plant roots and root exudates in earthworm feeding and nutrition, yet it is likely to be important for both soil- and litter-feeding species, although the former incorporated little root carbon in maize fields (Albers *et al.*, 2006). Grazing on root hairs in soil has been observed directly (Gunn & Cherrett, 1993) and traces of root hairs have also been detected in the gut (Baylis, Cherrett & Ford, 1986). Actual assimilation of carbon by earthworms from roots or rhizodeposits in a grassland soil (Ostle *et al.*, 2007) or fine tree roots and associated mycorrhiza has only recently been quantified by using ^{13}C labelling methods (see below; Gilbert *et al.*, 2014).

Novel methods and analytical approaches have provided new insights into the nuanced feeding ecology of earthworm species and the actual nutritional contribution of dietary components. Stable isotope analysis (^{13}C and ^{15}N) made it possible to identify assimilated dietary components rather than ingested materials (i.e. soil). Bulk isotope analysis has been used successfully to differentiate the diet of co-existing earthworm species ranging from fresh litter to soil organic matter (Martin, Balesdent & Mariotti, 1992; Schmidt, Scrimgeour & Handley, 1997; Scheu & Falca, 2000). This technique also elucidated the trophic position of earthworm species of as yet unknown ecology (Uchida *et al.*, 2004) and of species that invaded new ecosystems (Zhang *et al.*, 2010; Melody & Schmidt, 2012). Stable isotope measurements of specific compounds (fatty acids) suggested that epigeic earthworms assimilate recently fixed carbon, while endogeics can assimilate recalcitrant carbon sources (Ferlian *et al.*, 2014). Compound-specific analysis of essential amino acids indicated that endogeic earthworms derive substantial proportions of amino acids from soil bacteria (Larsen *et al.*, 2016a, b; Potapov *et al.*, 2019c). Analysis of fatty acid composition alone (i.e. without isotopic measurements) may also allow detection of basal resources of earthworms such as bacteria and fungi, yet these methods have not been used widely (Sampedro, Jeannotte & Whalen, 2006; Ruess & Chamberlain, 2010). Isotope $^{13}CO_2$ tracer studies revealed that endogeic earthworms assimilate substantial amounts of carbon from microscopic soil algae and cyanobacteria (Schmidt, Dyckmans & Schrader, 2016b), representing a novel carbon input route into soil food webs independent of higher plants. Similarly, tracers showed that endogeic earthworms exploit labile soil carbon sources (Shilenkova & Tiunov, 2015). The abundance measurement of radiocarbon (^{14}C) by accelerator mass spectrometry is an expensive but powerful technique allowing estimation of the age of carbon assimilated by earthworms (Hyodo *et al.*, 2012). Such measurements have shown elegantly that epigeic earthworms assimilate younger carbon (typically less than 3 years old) compared to endogeic earthworms (about 5–10 years old) (Hyodo *et al.*, 2012); however, this is likely a mixed signal of carbon of different ages.

Overall, the food resources, trophic position and functions of litter-feeding earthworms as detritivores is fairly straightforward (de Ruiter *et al.*, 1993). The position of soil-feeding earthworms is harder to define and various techniques applied to date have shown that many different components contribute to their diet including dead plant matter, living roots, seeds, algae, bacteria, fungi, protists and nematodes. Most earthworm species appear to be opportunistic, eating both litter fragments and mineral soil, and hence their trophic status is difficult to define. Nevertheless, the isotope evidence strongly suggests that endogeic earthworms feed mainly on microbially processed organic matter, but how they unlock protected soil C is still unknown. The main knowledge gaps relate firstly to the role of microbes in earthworm nutrition, both for microbes in gut material (Egert *et al.*, 2004) as well as those attached to the gut wall (Thakuria *et al.*, 2010), and secondly to the mechanisms of mechanical digestion and physical release of soil C in their digestive track (Curry & Schmidt, 2007). Given their long evolutionary history living close together, the interactions between earthworms and plant roots are also a major knowledge gap, for example the nutritional exploitation of rhizodeposits by earthworms (Curry & Schmidt, 2007).

Despite their large body size, earthworms are prey for many invertebrate and vertebrate taxa. Among soil- or soil-surface dwelling invertebrates, larger predatory insects such as carabid and cantharid beetles are known to prey on earthworms (Harper *et al.*, 2005; Eitzinger & Traugott, 2011). Land planarians have generated attention as earthworm predators since they became invasive (Cannon *et al.*, 1999). An example is the 'New Zealand flatworm', *Arthurdendyus triangulatus*, which appears to prey preferentially on anecic earthworm species (Murchie & Gordon, 2013). In general, however, there is limited knowledge on species-specific predation on earthworms in soil food webs. Pollierer *et al.* (2009) suggested that large earthworms are 'trophic dead ends' because of the paucity of belowground invertebrate predators able to conquer them, leading Schwarzmüller, Eisenhauer & Brose (2015) to call them "trophic whales". Moles are specialised belowground mammalian predators of earthworms, preferentially feeding on large earthworm species (Funmilayo, 1979). Earthworms are also major dietary components for several aboveground vertebrate taxa, including wild boar, badgers, shrews, foxes, snakes and frogs (Kauhala, Laukkanen & von Rege, 1998; Schley & Roper, 2003; Reguera *et al.*, 2011). A recent study even showed that earthworms constitute a major dietary component for domestic cats in Paris suburbs for most of the year (Castaneda, Zarzoso-Lacoste & Bonnaud, 2020). Of major interest for the conservation of birds is the fact that many birds feed on earthworms, including many farmland and meadow birds (Peach, Robinson & Murray, 2004; Onrust *et al.*, 2019), waders in wetlands (Leito *et al.*, 2014) and owls (Livezey, 2007). Finally, it should be mentioned that earthworms are also hunted and collected by humans, either for their own diet (Marconi *et al.*, 2002) or for use as bait for fishing (Mitra *et al.*, 2009).

(*b*) *Enchytraeidae*

Key message: enchytraeids are detritivores. For some of them, dead plant material is the direct food, for others plant remains are a supplement for a microbial diet.

Enchytraeidae are commonly referred to as pot worms. This name describes them perfectly as ubiquitous creatures that can be found even in small plant pots. Despite this, the ecology of Enchytraeidae is less well known than that of their larger relatives, earthworms. There are approximately 760 species described (Timm & Erséus, 2021), but their diversity is also rarely studied due to difficulties in distinguishing the species (Pelosi & Römbke, 2017). The mean length of enchytraeid worms is about 1–2 cm (Coleman & Wall, 2015), however there are several very common species with an average size of an adult worm of 5–9 mm (*Enchytraeus buchholzi*, *Fridericia bulboides*) and even 1.5–3 mm (*Enchytronia parva*) (Schmelz & Collado, 2010). Enchytraeidae live in the top soil layers, and are involved in the decomposition of dead plant material and nutrient cycling in soils (Hendrix *et al.*, 1986; van Vliet, Beare & Coleman, 1995). Their occurrence depends mainly on soil moisture, organic matter content and pH (Brussaard *et al.*, 2012); they are abundant in wet acidic soils, especially in boreal forests and tundra (Wolters, 1988), but also in grasslands and arable fields (Pelosi & Rombke, 2017). In temperate boreal forests they can represent up to 20% of the total biomass of soil animals, and in tundra habitats even up to 50% (Petersen & Luxton, 1982).

Most Enchytraeidae are saprophagous, or at least considered to be saprophagous (Schlaghamerský & Krawczynski, 2015). Enchytraeidae were classified by Gajda, Gorgon & Urbisz (2017) into two trophic groups: primary decomposers and secondary decomposers. For primary decomposers, dead plant material is the major food (Latter, 1977; Latter & Howson, 1978). This group includes representatives of *Cognettia sphagnetorum sensu lato*, a dominant species group found across cold-climate soils (Gajda *et al.*, 2017). For secondary decomposers, plant remains are only part of the diet, which also includes microorganisms; their main food is bacteria (Krištüfek *et al.*, 1995). The importance of bacterial feeding in Enchytraeidae was confirmed by compound-specific analysis of essential amino acids (Larsen *et al.*, 2016a). Microscopic fungi can also be a substantial food resource for some species, e.g. *Fridericia* spp., *Enchytraeus* spp. and part of the *Cognettia sphagnetorum* species group (Hedlund & Augustsson, 1995; Larsen *et al.*, 2016b). Sapro-microphytophagous Enchytraeidae are also included as secondary decomposers. Microscopic algae constitute the primary source of food for *Mesenchytraeus solifugus*, the so-called 'ice worm' (Goodman, 1971; Murakami *et al.*, 2015). Enchytraeidae ingest food along with soil particles (Haimi & Siira-Pietikäinen, 2003), thus consuming mixed microscopic prey (Gajda *et al.*, 2017). Even feeding mostly on microorganisms, secondary decomposers stimulate plant litter degradation by digesting and digging activity (Puppe *et al.*, 2012; John *et al.*, 2019). Enchytraeidae assimilate nitrogen from plant litter (Caner *et al.*, 2004). Dead and living nematodes have been found in the digestive tract of Enchytraeidae (Dash, 1973), but the importance of nematodes in comparison to other food resources for Enchytraeidae is unknown. Stable isotope analysis has been little used for investigating the position of Enchytraeidae in soil food webs. Schmidt *et al.* (2004) showed that the large enchytraeid species *Fridericia galba* and the medium-sized *Fridericia christeri* were isotopically similar to endogeic earthworms, while the small *Enchytraeus buchholzi* was more enriched in ^{13}C and more depleted in ^{15}N, suggesting a specific trophic niche. In a recent study by Briones *et al.* (2020), Enchytraeidae as a group were found to be isotopically similar to anecic earthworms.

Enchytraeidae are prey for predatory nematodes, centipedes, adult ground beetles and other insects [Rhagionidae, Dolichopodidae, Elateridae (Didden, 1991; Ulrich & Schmelz, 2001)]. Gamasid mites also feed on Enchytraeidae, but may not significantly affect their abundance (Huhta, Sulkava & Viberg, 1998). Overall, a system of functional traits in Enchytraeidae is not yet established, so an important scientific task will be to determine the correlation between Enchytraeidae species' functional traits and their ecological functions. Jänsch, Römbke & Didden (2005) classified enchytraeid species with respect to abiotic factors such as soil moisture, pH and salinity (soil horizon and humus-form preferences) as well as life form and reproductive strategy. However, these data are incomplete and do not include food preferences.

(*c*) *Gastropoda*

Key message: soil-associated snails and slugs feed predominantly on microbes associated with dead plant material, however, they also consume living plants, lichens, fungi and even other invertebrates. Shells provide protection for snails vulnerable to specialised predators. Mucus provides protection for both snails and slugs.

Terrestrial gastropods are one of the most successful and diverse groups of animals on the planet (Barker, 2001) with an estimated 25,000 extant species (Rosenberg, 2014). Despite their likely importance, there is a dearth of publications focusing on the role of terrestrial gastropods in soil food webs. However, based on direct observations, faecal/gut analysis and food-choice tests, we know that snails and slugs feed on a wide range of food resources including living plants of all development stages from pollen, seeds, seedlings and wood to senescing plants including leaf litter, other animals (both living and dead) including their faeces, fungi, lichens, algae and even soil (Pallant, 1969, 1972; Mason, 1970a,b; Jennings & Barkham, 1975; Cook & Radford, 1988; Speiser, 2001; Barrada, Iglesias & Castillejo, 2004; Türke *et al.*, 2010; Cordoba, Millar & Mc Donnell, 2018). Thus, they can be considered as herbivores, omnivores, carnivores and detritivores, but the majority of terrestrial gastropods are microbivores feeding on microbes associated with decaying plants and animals (Speiser, 2001). Gastropods themselves have been recorded as prey for various predatory invertebrates including beetles and fly larvae (Barker, 2004). Terrestrial gastropods encompass epedaphic (e.g. *Lehmannia marginata*), hemiedaphic (e.g. *Deroceras reticulatum*) and euedaphic species (e.g. *Selenochlamys ysbryda*).

Although novel methods and analytical approaches yielded important insights into the feeding ecology of many soil invertebrates, they have been used little to date to study the diet of terrestrial gastropods. For example, with very few exceptions (Waterhouse, Boyer & Wratten, 2014) DNA analyses have not been utilised to improve our understanding of the diet of terrestrial gastropods and their role in soil food webs. However, numerous gut content studies have shown that gastropods are an important prey item for many predatory invertebrates such as Carabidae (Barker, 2004). Likewise, fatty acid analysis has been employed rarely for analysis of the diet of terrestrial gastropods, whereas in aquatic taxa it has enabled distinction between the use of autochthonous and allochthonous resources (Lau, Leung & Dudgeon, 2009; Shilla & Routh, 2017).

Stable isotope analyses have been applied more widely and provided evidence for food partitioning among terrestrial gastropods, indicating that snail and slug species may occupy distinct trophic niches and helping to explain their co-occurrence (Meyer & Yeung, 2011; Bonkowski & Kappes, 2018). Dual stable isotope analysis (δ^{13}C and δ^{15}N) has also provided evidence that the diet of certain gastropod species changes with season (e.g. from living plants to decaying plants) and developmental stage (Schmidt *et al.*, 2004; Bonkowski & Kappes, 2018). Such ontogenetic niche shifts may be an evolutionary adaptation to minimise competition between parents and offspring in soil food webs. In forest ecosystems, the presence of palatable fungi appears to be an important factor and the majority of slugs participate in a fungus-enhanced detritus food web (Bonkowski & Kappes, 2018). The latter study also demonstrated that high δ^{15}N values do not necessarily indicate predatory feeding (as was assumed by Meyer & Yeung, 2011), but can rather signify fungivory. In addition, differences in stable isotope ratios from the same gastropod species in different locations support the idea of flexible nutrition as a response to resource availability (Bonkowski & Kappes, 2018). The snail shell provides a useful target for studies on stable carbon isotope ratios. It has been demonstrated that shell carbonate ^{13}C/^{12}C ratios are influenced primarily by food and can provide information on the relative contribution of C3 and C4 plants to their diet (Goodfriend & Ellis, 2002; Metref *et al.*, 2003; Baldini *et al.*, 2007). Using isotopic tracers, Schmidt *et al.* (2016b) demonstrated that photoautotrophic microorganisms do not form an important component of the diet of *Deroceras reticulatum* in arable soils under laboratory conditions, but this is likely to differ in other gastropod taxa such as Succeinidae (Rory Mc Donnell, personal observations).

For future research, we suggest utilisation of fatty acid analysis and both molecular and metabolomic gut content analysis to deepen our understanding of the role of terrestrial gastropods in trophic interactions in soil food webs. Future isotope-based studies should include a greater variety of resources including living plants, leaf litter, seeds, wood, faeces, dead invertebrates, fungi, lichens and algae, in addition to investigating seasonal changes and dietary shifts. The overall importance of gastropods in soil food webs should be re-evaluated considering quantitative methods for collecting them.

(5) **Vertebrates**

(*a*) *Amphibians*

Key message: amphibians feed on a wide range of soil invertebrates. Due to their high density and biomass in moist tropical and temperate ecosystems, amphibians can greatly affect the abundance and composition of invertebrate communities and indirectly impact soil functioning.

Amphibians (Amphibia) are mostly small-sized ectothermic vertebrates distributed worldwide from tropical to temperate zones. The extant amphibian diversity is represented by a total of more than 8400 species (Frost, 2021). Adult amphibians are predators occupying high trophic positions in terrestrial food webs and feeding mostly on invertebrate prey (Kupfer *et al.*, 2006). Due to physiological constraints, amphibians typically avoid arid regions, are often associated with freshwater ecosystems and commonly display nocturnal activity.

By far the most abundant amphibians are frogs and toads (Anura, tailless amphibians), most of which are terrestrial and litter-dwelling. Terrestrial salamander-like amphibians (Caudata) are less diverse and are distributed only in the Northern Hemisphere. Both reach maximum diversity and density in tropical forests, where they are the most numerous terrestrial vertebrates (Scott, 1976; Inger, 1980; Petranka & Murray, 2001). These two groups adopt active foraging or sit-and-wait strategies (Wells, 2007) and consume a wide spectrum of invertebrates including insects and their larvae (coleopterans, ants, termites, orthopterans, dipterans, springtails and others), spiders, mites, molluscs, woodlice, millipedes, earthworms and sometimes crabs [e.g. salamanders (Burton, 1976; Gunzburger, 1999; Roner *et al.*, 2020); frogs (Labanick, 1976; Premo & Atmowidjojo, 1987; Werner, Wellborn & McPeek, 1995; Le *et al.*, 2018)]. They can be markedly selective in prey categories, with some species specialising on ants or termites, or generalists that prey on relatively large arthropods (Toft, 1980, 1981; Caldwell, 1996; Anderson & Mathis, 1999; Parmelee, 1999; Paluh *et al.*, 2015). Terrestrial amphibians are referred to as top predators in some forest soil food webs (Best & Welsh, 2014) and may exert a strong effect on soil invertebrates and nutrient recycling in forest ecosystems (Davic & Welsh, 2004). Field experiments showed that litter-dwelling salamanders and frogs may directly affect the composition of soil invertebrate communities (Wyman, 1998; Walton, Tsatiris & Rivera-Sostre, 2006; Walton, 2013) and indirectly influence litter decomposition and nutrient cycling (Beard, Vogt & Kulmatiski, 2002; Beard *et al.*, 2003; Semlitsch, O'Donnell & Thompson, 2014). Stable isotope analysis (δ^{13}C and δ^{15}N) was used to demonstrate ontogenetic shifts of anurans from primary consumers to higher trophic levels (Trakimas *et al.*, 2011; Huckembeck *et al.*, 2014) and to reveal the feeding specialisation of coexisting frog species (Araújo *et al.*, 2007).

Fossorial limbless amphibians (caecilians, Gymnophiona) represent a less-abundant group with a pantropical distribution. Rare dietary studies showed that caecilians forage underground at depths usually ranging from 10 to 60 cm (Wake, 1980; Kupfer, Nabhitabhata & Himstedt, 2005) or in leaf-litter and feed mostly on earthworms, molluscs, ants, termites and other soil invertebrates, with some species displaying trophic specialisation (O'Reilly, 2000; Measey & Gaborieau, 2004; Kupfer *et al.*, 2005, 2006; Ngo, Hoang & Ngo, 2014). Coexisting species were shown to partition their food resources (Jones, Loader & Gower, 2006; Kouete & Blackburn, 2020). Given the apparently high density of some caecilians (up to 1.9 ind. m^{-2} locally; Measey *et al.*, 2003), their impact on soil invertebrate communities and especially earthworm populations can be substantial in some ecosystems (Measey & Gaborieau, 2004; Jones *et al.*, 2006).

Overall, terrestrial amphibians can be considered as generalist macroinvertebrate predators in most soil food webs. The following trophic groups can be distinguished: litter-dwelling anuran and caudate amphibians feeding on social insects (ant/termite specialists) or on a wide spectrum of invertebrate prey (generalists), and fossorial caecilians consuming diverse soil-dwelling invertebrates, including endogeic earthworms. Given the recent critical decline of amphibians across the world due to the chytridiomycosis pandemic and other factors (Wake, 1991; Collins, 2010), future studies should explore the ecological consequences of amphibian extinction for soil communities.

(*b*) *Reptiles*

Key message: *squamate reptiles are mostly diurnal predators or omnivores that occupy high trophic levels in terrestrial food webs and play important roles in controlling invertebrate communities*, *especially in arid and semiarid habitats*.

Among non-avian reptiles, scaled reptiles (Squamata) – especially lizards, which include about 7140 species and form the most diverse and speciose group directly involved in soil food webs (Uetz, Freed & Hošek, 2021). Lizards are mostly small- to medium-sized ectothermic vertebrates that inhabit all kinds of terrestrial habitats and are particularly well adapted to arid conditions and strong insolation. Most lizards are predators that prey on invertebrates, although plant food is often present in their diet. Vitt *et al.* (2003) define the following important prey categories: ants, beetles, orthopterans, non-ant hymenopterans, insect larvae, pupae and eggs, spiders and termites. Feeding specialisation is based on activity types (nocturnal in most Gekkota and diurnal in most other groups), foraging style (ambush hunters or active foragers), sensory mechanisms of prey detection (visual, chemosensory or both) and prey prehension (by the tongue or jaws) (Pianka, Pianka & Vitt, 2003; Vitt *et al.*, 2003). Species inhabiting arid regions tend to specialise on ants and termites (Abensperg-Traun & Steven, 1997). Partitioning of food resources may occur among coexisting lizard species (James, 1991; Vitt *et al.*, 2000; Luiselli, 2008; Murray *et al.*, 2016). Terrestrial lizards occupy high positions in terrestrial food webs, being top predators in desert, grassland and insular ecosystems (Spiller & Schoener, 1990; Östman *et al.*, 2007; Des Roches, Harmon & Rosenblum, 2016). In tropical forests, they occupy a similar trophic level to that of litter-dwelling amphibians (Inger, 1980; Vitt & Caldwell, 1994). Taking into account the great diversity and abundance of lizards, especially in desert, semiarid and insular communities, they can have a major impact on ecosystem resources (Morton & James, 1988; Buckley & Jetz, 2007; Vargas-García *et al.*, 2019). Field experiments revealed that lizards can substantially affect the density and composition of soil invertebrate communities, mainly by reducing the abundance of their target prey groups (Spiller & Schoener, 1988; González-Suárez *et al.*, 2011). Stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$) ratios were used to reveal the basal plant food sources in the food chains involving diverse lizards (Magnusson *et al.*, 2001; Pringle & Fox-Dobbs, 2008) and to study interpopulation ecological divergence within lizard species (Vidal & Sabat, 2010; Des Roches *et al.*, 2016).

Fossorial and subfossorial species evolved in many phyla of Squamata (Vidal & Hedges, 2005; Gauthier *et al.*, 2012) and have a wide distribution. Highly specialised for burrowing, amphisbaenians (Amphisbaenia) and blind snakes (Scolecophidia) are strict predators specialising on soil invertebrates. Amphisbaenians feed in the soil at a depth of about 10–20 cm (Gomes *et al.*, 2009); most species are generalists, but some are rather selective in their prey, preferring termites, ants, coleopteran larvae, earthworms (Kearney, 2003; Gomes *et al.*, 2009) or even hard-shelled gastropods (Martín *et al.*, 2013; Baeckens *et al.*, 2017). Blind snakes mostly specialise on ant larvae and pupae, with some rare species selecting termites or earthworms (Webb & Shine, 1993; Torres *et al.*, 2000; Webb, Branch & Shine, 2001). Although typical snakes (Alethinophidia) specialise mostly on vertebrate prey, some groups are adapted to feed on earthworms and gastropods (Macdonald, 1983).

In sum, squamates and especially lizards represent a very diverse group of predatory vertebrates that play crucial roles in a wide range of ecosystems worldwide. Often, they form multispecies communities that constitute the top trophic level in soil food webs, including those in desert, high-mountain, coastal and other ecosystems with extreme temperatures and arid conditions. Seasonal dietary changes, resource partitioning and the quantitative impact of lizards on soil communities in extreme habitats will be interesting avenues for future research.

(*c*) *Birds*

Key message: *insectivorous birds are mostly diurnally active and have a high metabolic rate*, *consuming large quantities of mainly aboveground*, *but in certain species also belowground invertebrates*, *thereby controlling their densities in ecosystems varying from tropical forests to subpolar tundra*.

Birds represent a highly specialised group of endothermic vertebrates numbering about 10,912 species (Gill, Donsker & Rasmussen, 2021) with a worldwide distribution. Distinctive features of birds include the ability to fly (i.e. high mobility), a tendency to form massive congregations, strong seasonality of reproductive cycles and massive migrations, mostly visual food searching and a high metabolic rate. Bird densities can reach up to 300–3500 individuals per km^2 depending on the habitat type (Gaston, Blackburn & Goldewijk, 2003). The majority of bird species feed on invertebrates – mostly arthropods, but also molluscs, terrestrial crustaceans and earthworms (Lopes *et al.*, 2016). An ontogenetic change in diet is found in many frugivorous, granivorous and omnivorous species, whose nestlings are reared mostly on invertebrates (Remsen Jr., Hyde & Chapman, 1993). Among arthropods, the most consumed prey taxa are insects (especially Lepidoptera, Coleoptera, Orthoptera, Diptera, Hemiptera and Hymenoptera) and Araneae (Wilson *et al.*, 1999; Sam *et al.*, 2017).

The birds most involved in soil food webs are those that feed at the soil surface. These can be separated into several guilds: (*i*) omnivorous ground foragers, such as pheasants and lyrebirds that feed on plants, fungi and invertebrates, (*ii*) insectivorous ground-gleaners like thrushes and babblers that collect invertebrates from the ground surface, and (*iii*) ground-probers such as woodcocks and other sandpipers that extract invertebrates by probing the soil or leaf litter with their bill (De Graaf, Tilghman & Anderson, 1985; Pearman, 2002; González-Salazar, Martínez-Meyer & López-Santiago, 2014). Based on global estimates, in open habitats, that is savannas, grasslands, deserts, croplands and Arctic tundra, birds consume ≥100 million tons of invertebrates per year, and ≥300 million tons in forest habitats (Nyffeler, Şekercioğlu & Whelan, 2018). Field experiments showed that birds are important in the control of soil invertebrates in tropical forests (Dunham, 2008). On sub-Antarctic islands, birds consume around 8% of the macroinvertebrate biomass annually (Burger, 1978). In tropical savannas, birds depend strongly on termites as the main food resource (Korb, 2000; Moe *et al.*, 2017). Some ground-feeding birds (waders, gulls, corvids, thrushes, pittas and others) specialise in feeding on earthworms; soil-probing waders can extract them from a depth of 3–5 cm or even deeper (Macdonald, 1983; Plum, 2005). As a whole, bird predation causes top-down trophic cascades and plays an important role in ecosystems (Bael *et al.*, 2008; Whelan, Wenny & Marquis, 2008; Mäntylä, Klemola & Laaksonen, 2011).

Some ground-feeding forest birds flake leaf-litter using their bill or scratch with their feet while foraging (Remsen & Robinson, 1990). Such litter disturbance may affect large areas, for example in Australia foraging lyrebirds turn over the whole forest floor every 20 months (Ashton & Bassett, 1997), and some other passerines completely turn over the litter in their habitat every 5 weeks (Theimer & Gehring, 1999). This disturbance greatly affects plant seed germination and the whole soil ecosystem (Theimer & Gehring, 1999; Eldridge & James, 2009). Seabirds, which feed on marine fish, affect soil invertebrates by the addition of extra nutrients to the soils around their colonies (Markwell & Daugherty, 2002).

Recent studies using stable isotope analyses (δD, δ^{13}C and δ^{15}N) have variously focused on food resource partitioning (Herrera *et al.*, 2003; Symes & Woodborne, 2010), dietary shifts in long-distance migratory birds (Rubenstein *et al.*, 2002; Hobson, 2005; Inger & Bearhop, 2008) and birds in human-modified landscapes (Ferger *et al.*, 2013; Hamer *et al.*, 2015; Otieno & Frenette, 2017). Overall, ground-foraging insectivorous birds play an important role in controlling the density of soil invertebrates in a wide range of ecosystems. By feeding on herbivorous macroinvertebrates, they function as effective biological control agents of pest species. Further research could investigate the influence of birds on the productivity of soil invertebrate communities, especially in the areas of high bird densities where their seasonal impact on ecosystems may be maximal, and on pedogenic processes.

(*d*) *Mammals*

Key message: *mammals are among the most important vertebrate groups in soil food webs. Highly specialised and opportunistic insectivores consume large quantities of soil invertebrates, controlling their abundance and composition. Fossorial species affect soil processes and functions by soil bioturbation.*

Mammals (Mammalia) are endothermic vertebrates with vastly diverse morphology and ecology with around 6567 living species (Mammal Diversity Database, 2021). Except for large herbivores and predators that affect soil biota mostly through the turnover of plant matter, defecation and as carrion, most small and medium-sized predatory and omnivorous mammals are tightly linked to soil food webs. Within the only flying group, predatory bats (Chiroptera) feed on aerial insects, many of which spend part of their life cycle in soil; classic diet studies as well as stable isotope and radiocarbon methods have clarified that many insect-eating bats are trophically closely related to detrital food webs (Davison & Zubaid, 1992; Hyodo *et al.*, 2015; Ruadreo, Voigt & Bumrungsri, 2018).

Insectivore mammals (formerly 'Insectivora', now split into several orders), and especially Eulipotyphla which includes moles and shrews, exert the most pronounced top-down effects on soil food webs. Shrews (Soricidae) comprising about 460 species, including the world smallest mammal, prey on a variety of litter- and soil-dwelling invertebrates, including earthworms, myriapods, spiders, insects and their larvae (Churchfield, Hollier & Brown, 1991). Shrews often form multispecies communities and can reach extremely high densities up to 17,667 individuals per km^2 (Smallwood & Smith, 2001). Given their very high metabolic rates (Ochocińska & Taylor, 2005), shrew communities are estimated to consume up to 111,150 prey individuals per hectare per month, thereby strongly affecting biomass and composition of soil invertebrate communities (Buckner, 1964, 1969). Small mammalian communities (shrews and small rodents) may reduce the number of large invertebrates by 23–65% (Churchfield & Brown, 1987; Churchfield *et al.*, 1991). In tropical forests, shrews largely contribute to controlling the density of soil spiders, insects and earthworms (Dunham, 2008). Carbon and nitrogen stable isotope analyses have been applied to study trophic niche overlap and shifts in the community composition of shrews and small terrestrial rodents in a number of ecosystems (Symes *et al.*, 2013; Baltensperger *et al.*, 2015; Eckrich, Flaherty & Ben-David, 2018). DNA metabarcoding has allowed detailed investigation of diet composition and trophic interactions of terrestrial and semi-aquatic shrews (Biffi *et al.*, 2017; Browett *et al.*, 2021). Moles (Talpidae) are fossorial insectivores that feed mostly on earthworms, consuming them in large quantities, and are closely associated with their distribution (Raw, 1966; Funmilayo, 1977). Marsupial fossorial species convergent with moles are thought to have a wider diet (Pavey, Burwell & Benshemesh, 2012).

A number of taxa of relatively large mammals with highly specialised morphology are adapted to feed on social insects (ants and termites): echidnas (Monotremata) in Australasia (Griffiths & Greenslade, 1990; Abensperg-Traun & Boer, 1992), ant-eaters (Pilosa) in South America (Gallo *et al.*, 2017), the aardvark (Tubulidentata) in South Africa (Taylor, Lindsey & Skinner, 2002) and pangolins (Pholidota) in tropical Asia and Africa (Pietersen *et al.*, 2016). All these species are extremely selective in their prey types; they possess a highly derived feeding apparatus and are adapted to digging and massive extraction of insects. Armadillos (Cingulata) feed on a wide spectrum of terrestrial invertebrates, and some species are considered to be ant and termite specialists (Anacleto, 2007). Some large carnivorous mammals (Carnivora) also specialise on termite-eating. The diet of the aardwolf (Hyaenidae) consists almost exclusively of termites of the genus *Trinervitermes* (Cooper & Skinner, 1979; de Vries *et al.*, 2011) and the bat-eared fox (Canidae) also specialises on termites, although it is more flexible in selecting additional invertebrate prey (Jumbam *et al.*, 2019).

Ants and termites are also consumed opportunistically by numerous predatory or omnivorous mammals, including marsupials, rodents, primates, treeshrews and others (Redford, 1987; Abensperg-Traun & Steven, 1997). Seasonally, ants can form the bulk of the diet of bears (Noyce, Kannowski & Riggs, 1997). Other terrestrial arthropods, especially insects and their larvae, form an important part of the diet of mustelids (Clevenger, 1993), mongooses (Cronk & Pillay, 2019) and meerkats (Doolan & Macdonald, 1996). Earthworms are also key components in the diet of many mammalian carnivores, such as badgers, raccoons, foxes and viverrids (Macdonald, 1983).

Rodents represent another soil-associated group of mammals, including numerous fossorial species that can reach enormous population densities of 500–600 individuals per ha during outbreaks (e.g. McGuire *et al.*, 1993; Zhang, Zhong & Fan, 2003). Most rodents are omnivorous, sometimes with a predominance of invertebrates in their diet; thus, many of them may affect the composition of soil invertebrate communities (Zemanek, 1972; Houtcooper, 1978; Parmenter & MacMahon, 1988). Their impact on invertebrates is especially significant in cases of human-assisted invasions of rodents (mostly rats) into formerly rodent-free ecosystems (St Clair, 2011; Harper & Bunbury, 2015). Burrowing rodents, especially colonial murids and sciurids, affect soil ecosystems by bioturbation and have an important effect on soil development, especially in arid and semi-arid regions (Whitford & Kay, 1999).

Overall, ground-living and fossorial mammals preying on invertebrates form a major functional group in belowground food webs. Due to their large size or high population density combined with high metabolic rates, they consume large quantities of prey biomass in particular of social insects, insect larvae and earthworms, thereby regulating densities of abundant groups and functioning as ecosystem engineers, with strong effects on soil ecosystems and food webs. Further research could focus on the impact of native and invasive mammalian species on the structure, functioning and stability of belowground food webs, as well as the interrelationships between mammalian and invertebrate communities in ecosystems exposed to strong anthropogenic pressure.

III. SYNTHESIS AND PERSPECTIVES

(1) Multifunctional classification of belowground consumers

To develop an overarching multifunctional classification of soil consumers based on their feeding habits, we used an integrative taxonomic–ecological approach. First, we distinguished trophic groups individually within each taxonomic group because (*i*) identification of consumers, whether morphological or genetic, is based on taxonomy, and members of groups must be identifiable, and (*ii*) taxonomically defined groups usually share evolutionarily conserved traits (e.g. body mass, physiology, ingestion mode, reproductive strategy) that may be combined in integrative classifications. A taxon-independent classification of all soil consumers may comprise conventional trophic groups like 'fungivores', 'herbivores', 'bacterivores' and 'predators'. However, such a classification omits other traits and does not provide any information on how to classify a particular species to a particular trophic group. The integrative approach also allowed us to incorporate existing functional classifications in various groups even though they are based on different criteria.

Within the considered taxonomic groups very few species are specialised feeders, indicating that omnivory and generalist feeding is widespread in soil food webs (Scheu, 2002; Digel *et al.*, 2014). To reflect this trophic diversity, in many cases we assigned multiple consumer–resource relationships to individual trophic groups. For quantifying resource preferences, we classified resources for each group as either primary (resources representing major components of the diet of many species in the group), auxiliary (resources representing non-obligatory and minor components of the diet, but often present across species) or negligible. For each group, we also compiled information on key traits including body size, vertical stratification, key predation and defence traits, specific trophic interactions and stoichiometry. If judged by experts as important, these traits were also used to distinguish the group from other groups in the taxon. For example, classifications primarily related to vertical distribution were used for springtails, earthworms, centipedes, some vertebrates and mites. Classifications related to defence traits were used for gastropods and some mite groups. In so doing, we extended the common focus on food resources in previous classifications, as necessary to provide a solid basis for realistic food-web reconstructions considering at least body size and spatial distribution of soil organisms (Potapov, 2021; Potapov *et al.*, 2021b).

Our suggested classification is summarised in Fig. 1 and provided in full as online Supporting Information in Table S1. It provides 1–3 hierarchical levels of trophic groups for each taxonomic group. Classifications at different hierarchical levels are linked to the same set of parameters and can be used simultaneously, depending on the precision of taxonomic identification for different taxa (e.g. 'Orthoptera: Ensifera: Omnivores' represents an example of a three-level hierarchical classification). Fig. 1 provides a general overview of the trophic groups at the highest hierarchical level, representing the 30 most dominant taxa of soil consumers. The full classification is more complex and includes 148 trophic groups (see Table S1). Even at this more detailed resolution, trophic groups were often characterised by feeding on several resources, emphasising the prevalence of multichannel feeding in soil consumers (Scheu & Setälä, 2002; Digel *et al.*, 2014; Wolkovich, 2016; Potapov *et al.*, 2021b) (Fig. 1) and contrasting with traditional soil food-web reconstructions with distinct resource-based energy channels (Hunt *et al.*, 1987; de Ruiter, Neutel & Moore, 1994). Resource-based energy channels are not distinct in soil and the stability of soil food webs may be driven by mechanisms other than the bacteria–fungi balance in basal resources (Rooney *et al.*, 2006; Potapov, 2021).

(2) Applications and refinement of the multifunctional classification system

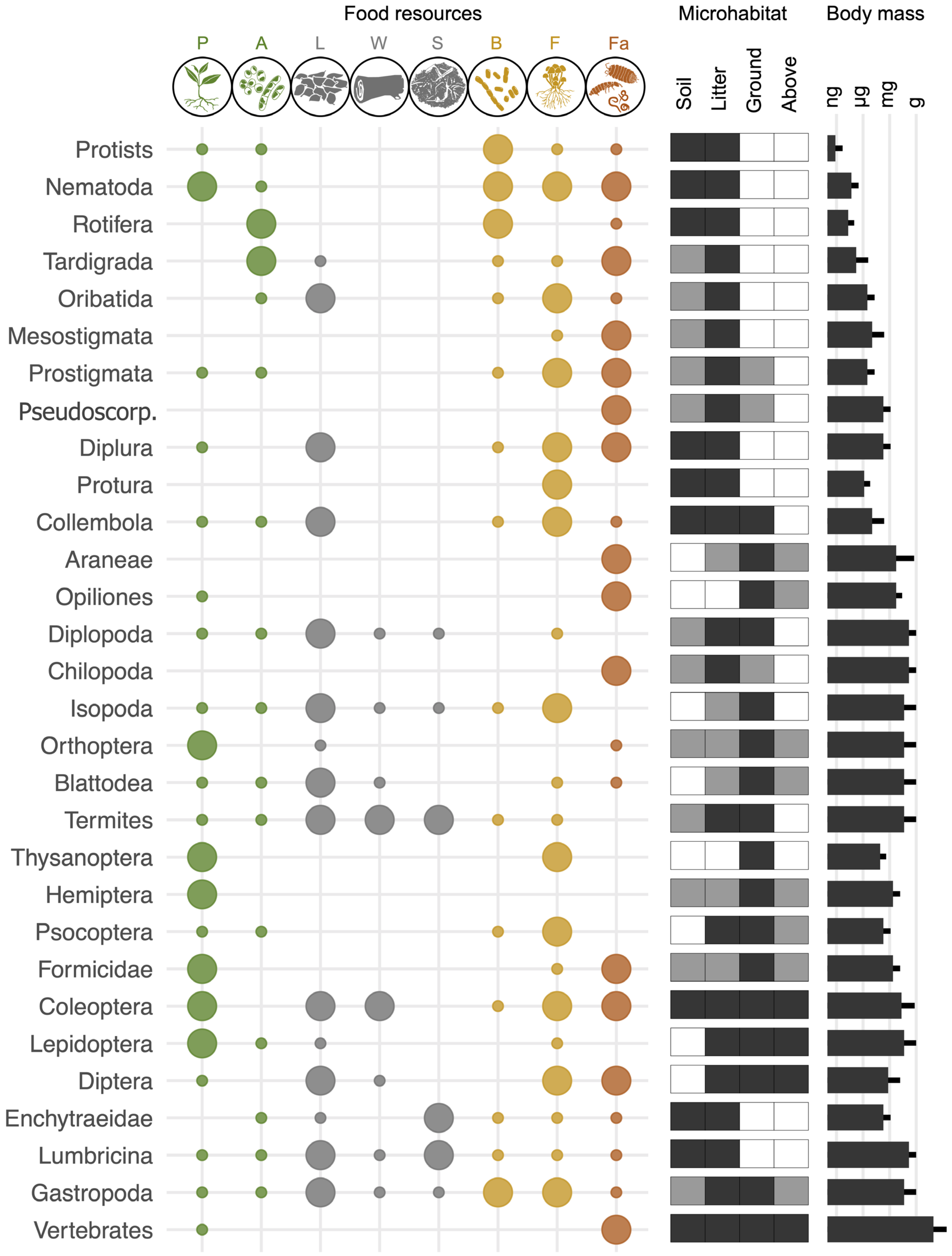
The multifunctional classification system presented above can be used to address a wide range of ecological questions regarding the assembly and functioning of soil consumer communities. The wide taxonomic scope of the classification is especially useful considering the shift towards multitaxon approaches in large-scale ecological projects and the increasing availability of comprehensive data sets on soil consumer communities (de Vries *et al.*, 2013; Geisen *et al.*, 2019; Zinger *et al.*, 2019; Delgado-Baquerizo *et al.*, 2020; Grass *et al.*, 2020; Potapov *et al.*, 2021b). The integrative taxonomic–ecological approach allows existing community data to be re-analysed using the suggested multifunctional classification (Burkhardt *et al.*, 2014; Johnston & Sibly, 2020; Guerra *et al.*, 2021).

As a basic application, this classification can be used to assess changes in abundance and biomass of different trophic groups across scales and ecosystems to infer changes in corresponding trophic functions and overall functional diversity. However, the most powerful use of this classification is to assess multifunctionality of soil consumer communities *via* a food-web approach. In an associated conceptual soil food-web review (Potapov, 2021), this classification and generic predator–prey interaction patterns were used to construct 'multichannel' soil food webs. This food-web model was further combined with energy flux approaches (Barnes *et al.*, 2014, 2018) to infer multiple ecosystem functions by consumer communities, for example litter transformation, herbivory and top-down control, and to assess rapid to slow energy channelling and spatial distribution of energy fluxes in soil food webs. A combination of the multifunctional classification with the energy flux approach allows analysis of communities from protists to vertebrates using a single metric, energy flux, and thus is a powerful tool for any multitaxon study.

Of course, the suggested classification needs to be developed further and refined. More trophic groups may need to be added using the same functional traits, trait values might be refined, or the trait list may need to be expanded. The most promising traits are active movement speed, passive dispersal mechanisms and reproductive strategy (*r*/*K*), but these are beyond the scope of this review, which focuses on feeding relationships. Additional knowledge on certain groups of soil fauna (e.g. Prostigmata) is particularly needed to elucidate feeding substrates and behaviours of their taxa to permit their division into more meaningful and coherent groups. The generic multifunctional classification presented here assumes that trophic niches of species shift little among ecosystem types (Klarner *et al.*, 2014; Potapov *et al.*, 2016b), but a given species or taxon can exhibit marked differences in resource use between contrasting environments (Krause *et al.*, 2019; Susanti *et al.*, 2019). The classification can be adapted to local communities by assessing body masses and feeding preferences empirically. Describing systematically observed differences within taxonomic groups between different ecosystems would be another step towards generalisation of the approach.

(3) What have we learnt from modern methods?

In the present review, we merged traditional (mostly observational) knowledge with new data collected using modern tools and evaluated the progress driven by these new methodologies (see Table 4). While such progress varies across individual taxonomic groups, there are universal advances. First, modern tools have allowed us to differentiate and evaluate the assimilation of different resource types, in addition to resource ingestion. This has been of particular importance for decomposer groups that feed on a mixture of detritus and microorganisms, such as Lumbricina, Diplopoda, Isopoda and Oribatida (Semenyuk & Tiunov, 2011a; Larsen *et al.*, 2016a; Potapov *et al.*, 2019c; Pollierer & Scheu, 2021). Second, modern tools have allowed us to quantify trophic links of soil consumers to different energy channels in soil food webs. This relates in particular to the root-based energy channel (Ostle *et al.*, 2007; Pollierer *et al.*, 2007; Goncharov *et al.*, 2016), fungal and bacterial energy channels (Larsen *et al.*, 2016a; Pollierer & Scheu, 2021), algae-based energy channel (Schmidt *et al.*, 2016b; Seppey *et al.*, 2017; Potapov *et al.*, 2018) and usage of carbon of different age (Hyodo *et al.*, 2006, 2015). Third, modern tools have allowed us to quantify trophic links of consumers to allochthonous food resources, for example aquatic subsidies to terrestrial consumers (Collier *et al.*, 2002; Korobushkin *et al.*, 2016) or detrital subsidies to aboveground consumers (Pringle & Fox-Dobbs, 2008; Hyodo, Kohzu & Tayasu, 2010a; Birkhofer *et al.*, 2011b; Hyodo *et al.*, 2015).



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Some of the insights provided by modern tools are related to the body size of taxonomic groups. DNA-sequencing approaches have significantly widened our knowledge on the trophic diversity of soil protists, and these approaches are essential to assess their diversity and its functioning, but isotopic and biochemical methods are difficult to apply (with the exception of stable isotope probing; for example Kramer *et al.*, 2016). For microfauna, modern tools have either confirmed the validity of traditional classifications (nematodes; Kudrin *et al.*, 2015), or have been applied rarely (e.g. rotifers and tardigrades). Progress here will depend on improving the resolution of such tools allowing to reduce the amount of tissue required for analysis. For dominant groups of mesofauna (e.g. springtails and mites), considerable progress has been achieved, with new and refined trophic classifications suggested (Maraun *et al.*, 2011; Potapov *et al.*, 2016b), the importance of alternative food resources (nematodes, bacteria, algae) emphasised (Heidemann *et al.*, 2014a; Ferlian *et al.*, 2015; Potapov *et al.*, 2018, 2021a) and processes of trophic niche differentiation and shifts quantified (Schneider *et al.*, 2004; Chahartaghi *et al.*, 2005; Klarner *et al.*, 2013; Birkhofer *et al.*, 2016b; Maraun *et al.*, 2020; Krause *et al.*, 2021). Finally, while the trophic classifications of macrofauna have remained largely the same, modern tools have allowed distinguishing assimilated from ingested components (Larsen *et al.*, 2016b) and have identified gradual niche differentiation among sympatric and morphologically similar species (Melody & Schmidt, 2012; Bortolin *et al.*, 2018). Modern tools also have been invaluable for the quantification of energy channelling from different resources by large-sized generalist feeders (Larsen *et al.*, 2016b; Mader *et al.*, 2018). The full potential of modern tools in soil trophic ecology is, however, yet to be exploited, in particular considering that these approaches have so far been applied only to a limited extent in many taxonomic groups that may be important ecosystem components (e.g. Diptera, Gastropoda, Prostigmata, Symphyla, Diplura, Pseudoscorpiones, Thysanoptera, Rotifera and Tardigrada). In addition, most of the available data are from temperate regions, which may bias the global perspective of the present review.

Across groups, modern tools have emphasised two seemingly contrasting patterns: omnivory and trophic niche differentiation. Many groups, from protists to large invertebrates that previously were assumed to feed on a single resource, have been proved to receive energy from multiple alternative food resources (Fig. 1). Feeding generalism of microbivores and predators was also identified and quantified for species-specific interactions using diagnostic PCA and next-generation sequencing approaches (Anslan *et al.*, 2018; Eitzinger *et al.*, 2019). At the same time, on the group level, modern tools have delivered strong evidence for trophic niche differentiation in taxa with apparently consistent feeding habits like springtails, oribatid mites and diplopods (Schneider *et al.*, 2004; Chahartaghi *et al.*, 2005; Semenyuk & Tiunov, 2011b; Ferlian *et al.*, 2015). Taken together, it is becoming evident that soil communities comprise mostly omnivores with different resource preferences, rather than resource specialists. The term "choosy generalists" was coined for oribatid mites (Schneider & Maraun, 2005), but it may well describe the dominant feeding behaviour across soil consumers in terms of species-specific, but also resource-specific interactions. Realistic reconstructions of soil food webs should reflect this feeding behaviour by depicting multiple consumer–resource interactions across trophic groups, while assigning larger interaction strengths to preferred resources (Fig. 1; Potapov, 2021).

(4) A need for accessible and interoperable trophic data

Our review cites almost a thousand papers that have explored feeding habits of soil consumers. And yet, this is only part of the data collected. Many taxonomic groups, such as oribatid mites, have complex but poorly phylogenetically constrained feeding habits (Schaefer & Caruso, 2019), meaning that well-resolved trophic classification in such groups is only possible at high taxonomic resolution such as at the genus or species level. And even when data on feeding habits are available for each species in a given community, these data will be dispersed across many publications. The compilation of such data for a wide range of taxa is an enormous task and generating new knowledge in a traditional way will be very laborious. So, can we improve future food-web reconstructions and keep up with current knowledge?

The example above demonstrates the need for open interoperable platforms that facilitate continuous updating of previous knowledge as well as integration of new data on ecological traits and trophic relationships, while making this

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Fig. 1. Overview of food resources, vertical distribution and body mass for dominant consumer taxa in soil. Food resources are assigned based on information provided in this review. Large dots denote primary resources, small dots auxiliary resources. Colours delineate energy channels: green, grazing [plants (P) and algae (A)]; grey, detrital [litter (L), dead wood (W) and soil (S)]; dark yellow, microbial [bacteria (B) and fungi (F)]; dark orange, carnivory [feeding on other consumers (fauna, Fa)]. Classification of the listed taxonomic groups refers only to soil-associated taxa and excludes primarily aboveground species. Preferred microhabitats are shown with dark shading. The 'ground' microhabitat indicates taxa that are active on litter, wood and stone surfaces. The 'above' microhabitat marks taxa that spend part of their life cycle aboveground (e.g. flying or living on green vegetation), but are involved in soil food webs as larvae or by predation on soil animals. Mean living body mass and its standard deviation are shown with black bars on a logarithmic scale. A more detailed classification including 148 trophic groups is provided in Table S1.

information easily available for researchers (Gallagher *et al.*, 2020). General and taxon-specific online databases on soil invertebrate traits in most cases do not include traits specifically related to feeding habits (Pey *et al.*, 2014; Sandmann, Scheu & Potapov, 2019). Such 'trophic traits' could include not only consumer–resource interactions, but also defence or mobility traits (e.g. Birkhofer *et al.*, 2017b) and quantitative data derived from direct observations, food-choice experiments, stable isotope, fatty acid, gut enzyme, gut visual and gut DNA analyses (Chen *et al.*, 2017; Birkhofer *et al.*, 2017a; Potapov *et al.*, 2021a). The development of a sustainable trophic trait repository requires a well-defined vocabulary, data standards, ontologies, handy tools and further dissemination of open science ideas among ecologists (Schneider *et al.*, 2019; Gallagher *et al.*, 2020; Lowe *et al.*, 2020). Here we have provided a synopsis of current knowledge and publications, and suggested a framework for how to align these data across soil consumers, from protists to vertebrates. Future integration of this framework into soil ecological studies will help us comprehensively to assess the function of soil communities, including protists and animals.

IV. CONCLUSIONS

(1) We comprehensively reviewed the feeding habits of soil consumers, from protists to vertebrates. We specifically focused on recent progress using modern tools and reviewed the roles of different taxonomic groups in soil food webs. Across many taxonomic groups and traditionally used trophic groups we found widespread evidence for feeding on multiple food resources, challenging traditional soil food-web models based on distinct resource-based energy channels. Despite this, different taxonomic groups show preferences for certain combinations of food resources, making it possible to delineate the trophic positions of these "choosy generalists" and illuminate the overall structure of soil food webs.

(2) We have developed an overarching multifunctional classification based on feeding preferences, body sizes and other key functional traits of belowground consumers, including protists, invertebrates and vertebrates. The classification considers feeding on multiple food resources and thus can be used for realistic food-web reconstruction, as exemplified in an associated conceptual review (Potapov, 2021). The classification forms the basis for further development, refinement and flexible expansion by adding more trophic groups and functional traits, especially for groups that could not be divided into finer groups due to limited present knowledge.

(3) Modern tools, such as stable isotope, fatty acid and molecular gut content analyses have uncovered previously hidden facets of the trophic relationships of soil consumers. They have allowed us to assess food assimilation in omnivores, to quantify links to different energy channels across multiple trophic levels of consumers, and to trace the use of allochthonous resources under natural conditions in the field. Modern tools have demonstrated both trophic flexibility and niche differentiation across virtually all groups of belowground consumers studied so far.

(4) DNA analyses have become a powerful tool to uncover cryptic functional diversity of soil protists, opening perspectives to describe the structure of soil food webs at the microscale. Stable isotope and fatty acid analyses are rarely applied to unicellular organisms due to technical limitations related to the minimum biomass required, but have been used successfully to refine trophic classifications of mesofauna and quantified the importance of alternative food/prey in their diet (nematodes, bacteria, algae). Trophic classifications of large soil consumers (macrofauna, vertebrates) were generally confirmed by modern tools, but these tools make it possible to quantify assimilation of food and to disentangle different energy channels in omnivores.

(5) Overall, the rapid progress triggered by modern tools and new ideas about the structure and functioning of soil food webs has been accompanied by the re-evaluation of the trophic ecology of many consumer groups in soil. We believe that the proposed multi-taxon classification will allow us to tackle the complexity of feeding interactions in soil in a new comprehensive way. Further progress is expected with wider adoption of modern tools and the accumulation of species-specific and group-specific data. Open interoperable platforms able to incorporate historical and new data including ecological traits and feeding relationships will be needed to facilitate this process and deliver the accumulating knowledge to a broad spectrum of researchers focusing on the ecology of soils and beyond.

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VII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Table S1. List of trophic groups of soil consumers with their functional traits.

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