Soil Biology and Biochemistry 177 (2023) 108890

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Perspectives Paper

New perspectives on soil animal trophic ecology through the lens of C and N stable isotope ratios of oribatid mites

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ARTICLE INFO

Keywords:
Soil mites
Trophic ecology
^{15}N
^{13}C
Niche differentiation
Diversity
Food web
Stable isotopes
Oribatida

ABSTRACT

Knowledge of the trophic ecology of soil animals is important for understanding their high alpha diversity as well as their functional role in soil food webs and systems. In the last 20 years, the analysis of natural variations in stable isotope ratios ($^{15}N/^{14}N$, $^{13}C/^{12}C$) has revolutionized our view on soil animal trophic ecology. Here, we review the state of the art of the trophic ecology of a highly abundant and diverse soil animal taxon, oribatid mites (Oribatida), investigated by stable isotope analyses. The review is based on 25 papers reporting stable isotope data of 292 oribatid mite taxa from 30 different sites. Four main findings emerged. (1) Oribatid mites cluster into six trophic groups, i.e. moss feeders, lichen feeders, primary decomposers, fungal feeders/secondary decomposers, predators/scavengers and marine algal feeders, plus one additional group, which incorporates $CaCO_3$ in their cuticle for defence but still belongs to the fungal feeders/secondary decomposers group. (2) Of the 292 species studied 43.7% were classified as fungal feeders/secondary decomposers, 27.0% as primary decomposers and 15.7% as predators/scavengers, only few species include $CaCO_3$ into their skeleton (6.1%), feed on lichens (4.9%), mosses (2.1%) or marine algae (0.7%). (3) In about one-third of the species studied the trophic niche was constant or varied little between sites or habitats, but in two-thirds of the species their trophic niche varied between habitats, with some species even shifting trophic levels, indicating trophic plasticity. (4) When aggregated at higher taxonomic level oribatid mite species clustered in only three instead of six trophic groups. This indicates that species within the same high level taxon often belong to different trophic groups, for example because feeding habits evolved convergently. Therefore, to accurately reflect the trophic ecology of oribatid mites their stable isotope signatures need to be analysed at species level. However, stable isotope analyses also have limitations, e.g. feeding on bacteria and fungi cannot be separated, and the same is true for feeding on ectomycorrhizal and arbuscular mycorrhizal fungi. Other methods such as fatty acid, amino acid and molecular gut content analyses as well as microbiome analyses may complement stable isotope studies and resolve oribatid mite trophic niche differentiation at a higher resolution. This will contribute to a better understanding of the local coexistence of large numbers of species in soil. Finally, we provide perspectives on how to integrate microarthropods into soil food webs using stable isotope and other methods allowing deeper insight into their trophic structure.

1. The primacy of trophic ecology and the aim of this study

The distribution, availability and accessibility of resources is key for understanding the occurrences and densities of animal species (White, 1993). The main activity of most animals is to acquire resources for growth and reproduction (Ejsmond et al., 2019). Usually, those resources are heterogeneously distributed and in limited supply resulting in local resource competition. However, this may not apply to resources that are temporarily (e.g., phloem sap during summer for aphids) or permanently (e.g., dead organic material for some decomposer taxa) available in excess. Populations of taxa using these resources may grow exponentially until these resources also eventually become limiting or until fluctuations in environmental factors hamper further increase in density (Tilman, 1982; Bluhm et al., 2016).

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https://doi.org/10.1016/j.soilbio.2022.108890
Received 15 June 2022; Received in revised form 7 November 2022; Accepted 15 November 2022
Available online 25 November 2022

For soil animals, the importance of resources as regulatory factor for population dynamics is intensively debated. On the one hand, key resources, especially dead organic matter, may not be limiting as it is replenished regularly in large amounts, e.g. in forests typically >90% of what is produced by plants enters the soil system as litter material, and arguably this is much more than soil animal population might need within the turnaround time of the resource. As competition for resources may be one of the factors for the dominance of sexual reproduction in the animal kingdom, ample resource supply in decomposer communities has been proposed to be responsible for the widespread parthenogenetic reproduction in soil animal taxa (Scheu and Drossel, 2007). On the other hand, certain resources may well be limiting in soil, for example certain fungal species for fungivores or prey species for predators that are not accessible or even defend themselves from consumption. Knowledge on resource use, limiting factors and niche differentiation of soil animals is of prime importance to understand (a) which factors are driving soil animal density and community composition, (b) why there are so many species of soil animals coexisting in a seemingly homogeneous habitat (Anderson, 1975), and (c) why there are so many parthenogenetic species in soil (Scheu and Drossel, 2007; Maraun et al., 2019). Generally, soil animals are assumed to be trophic generalists, which is likely due to the fact that searching for specific resources in the soil matrix is difficult and perhaps not even necessary (Scheu and Setälä, 2002; Digel et al., 2014; Erktan et al., 2020). Specialists need to easily find resources or even live on them as in parasites. In comparison to above the ground, sensing of and moving towards resources/prey species in soil is also much more restricted (Erktan et al., 2020).

Here, we use oribatid mites as model organisms to better understand resource use and niche differentiation in one of the major groups of soil invertebrates reaching high diversity and abundance in most soils across the world. Resource use and trophic ecology of oribatid mites has been studied for almost 100 years (Jacot, 1932; Schuster, 1956; Hartenstein, 1962; Siepel and de Ruiter-Dijkman, 1993; Schneider et al., 2004). Due to the small size of the animals and the opaqueness of soil, however, insight into their nutrition and trophic niches in their natural habitat remained limited resulting in the assumption that oribatids as a group are trophically rather uniform and predominantly feed on dead organic matter and associated fungi (Jacot, 1932, 1939; Schuster, 1956; Barreto and Lindo 2018; Wehner et al., 2018). This perception has changed fundamentally with the analysis of natural variations in stable isotope ratios ($^{15}N/^{14}N$, $^{13}C/^{12}C$) as markers for animal nutrition and trophic niches, opening new perspectives by showing that oribatid mite species span across the full range of trophic levels, which signals the existence of distinct and very different trophic niches.

Here, we report progress in understanding resource use and trophic structure of oribatid mites based on stable isotope studies by reviewing 25 papers including 292 oribatid mite taxa from 30 different sites. We summarize existing knowledge on oribatid mite trophic ecology before and after the use of stable isotope techniques (Sections 2 and 3), discuss limitations of the method (Section 4) and give an outlook on how to go beyond stable isotopes for understanding the trophic ecology of oribatid mites (and soil animals in general; Sections 5 and 6).

2. The pre-stable isotope era

Before the use of stable isotopes for understanding trophic niches of soil animal species and the trophic structure of soil animal communities, researchers used observational methods to investigate the trophic ecology of soil animals. In case of oribatid mites, first studies based on direct observations in the laboratory concluded that most species feed on dead organic matter (Jacot, 1932). Later Jacot (1936) and Gourbiere et al. (1985) noticed that some species of Phthiracaridae are not indiscriminately feeding on organic material, but that the juveniles feed inside needles which protects them against predation. Gut content analyses provided additional information on oribatid mite trophic ecology. Forsslund (1938) as well as Anderson (1975) reported that the gut content of oribatid mites comprises a variety of materials, but mainly litter material and fungal hyphae. Based on these observations, they concluded that fungi and litter are the main food resources of oribatid mite species; although they were aware that these conclusions have to be taken with care since the material in the gut may not be identical to the material that is assimilated. Indicating that the diet of oribatid mites indeed is more complex, Harding and Stuttart (1974) observed that they also ingest mosses, algae, lichens and pollen; and Riha (1951) noticed that Oppiidae and *Hypochthonius rufulus* feed on dead microarthropods, i.e. live as scavengers. The first grouping of oribatid mites based on their nutrition was done by Schuster (1956), who aggregated oribatid mites into three trophic groups, i.e. species feeding on dead organic matter (macro-phytophages), species feeding on fungi, lichens, algae and mosses (micro-phytophagous), and species feeding on both (non--specialists). This grouping was mainly based on feeding experiments, gut content analyses and morphology of chelicerae. Although being very coarse, it must still be viewed with caution since laboratory feeding experiments may not adequately reflect the diet in the field. Further, cheliceral morphology in most oribatid mite species is similar (except for e.g., Suctobelbidae, Gustaviidae and Phenopeloppidae which have sucking mouthparts) and, as stated above, the material in the gut does not necessarily represent what is actually assimilated. Similar attempts to group oribatid mites were later done by Wallwork (1958) and Kaneko (1988), but all these attempts also faced similar limitations. In the 1960s, researchers started investigating fungal feeding in oribatid mites in laboratory experiments (Hartenstein, 1962; Luxton, 1966). These early and later studies highlighted that oribatid mites prefer to feed on dark pigmented fungi ("Dematiacea") (Maraun et al., 1998; Schneider and Maraun, 2005), however, the reason for this preference remained unclear. In the 1970s researchers started using enzyme analyses to better understand the trophic ecology of oribatid mites (Zinkler, 1970; Luxton 1972, 1979). Based on those studies and further investigations Siepel and de Ruiter-Dijkman (1993) proposed five major trophic groups of oribatid mites: Herbivorous grazers, fungivorous grazers, herbi-fungivorous grazers, fungivorous browsers and opportunistic herbi-fungivores. However, using gut enzyme analyses for grouping animals in trophic groups also has limitations as it is difficult to separate the enzymes that are produced by the animals themselves from the enzymes that are taken up from the environment or produced by microorganisms in the gut. Additionally, the method only reflects digestion processes at time of sampling, which may not represent the diet variety of the animals in the long-term. The method, therefore, was not further used for studying trophic niches of oribatid mites. However, researchers started thinking about trophic plasticity in oribatid mites (Anderson, 1975), a problem that could not be investigated with the methods available at that time, but was taken up later using stable isotope analysis (Krause et al., 2021). Faced with the limitations of the methods available, trophic niche differentiation in oribatid mites remained elusive leaving "the enigma of soil animal species diversity" unresolved (Anderson, 1975). This issue and the other topics mentioned above were approached again with the first studies on the stable isotope ratios in oribatid mites (Scheu and Falca, 2000; Schneider et al., 2004). But a major conclusion already clearly emerged from all the pioneering studies: oribatids are not homogeneous in terms of what different species feed on and consist of species and taxa that may feed on very different items.

3. The era of stable isotope ecology

Freshwater and marine ecologists first used natural variations in stable isotope ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in animal species to better understand trophic niches and trophic structure of food webs (Hobson and Welch, 1992; France, 1995). Their work build on the findings by Minagawa and Wada (1984), Wada et al. (1991), DeNiro and Epstein (1981) and Post (2002) who established that ^{15}N in animal tissue is enriched by about 3.4 delta units (‰) per trophic level, whereas ^{13}C

typically is only little enriched (<1%). Stable isotopes do not decay into other elements and the rare stable isotopes of an element usually have more neutrons but the same number of protons compared to the more common stable isotope of that element. Hence, the rare stable isotope is heavier than the more common one and the chemical bonds of molecules containing heavy stable isotopes are stronger than those containing the lighter one of the same element. Therefore, molecules containing the heavier isotope react more slowly than the ones containing lighter isotopes resulting in fractionation. This also applies to consumers which preferentially excrete the lighter isotope resulting e.g., in the enrichment in the heavier isotope such as ^{15}N along food chains (Dawson and Brooks, 2001).

One of the first studies using stable isotopes (^{15}N) for analysing the trophic ecology of soil animals including oribatid mites was Scheu and Falca (2000). Their data indicated that soil food webs comprise about four trophic levels, and that the trophic niches of most taxa are surprisingly constant, i.e. independent of the actual location (soil depth) of the animal in the soil. Another important conclusion was that the trophic niches were not necessarily neatly defined, with gradients between niches. At the same time, Ponsard and Arditi (2000) analysed the food web structure of soil macro-invertebrates using ^{15}N and ^{13}C and concluded that the food web comprises only two trophic levels. In the following years, a number of studies used stable isotopes for analysing soil animal food webs, and oribatid mites featured prominently in these studies (e.g., Crotty et al., 2014). Those studies contributed considerably to a better understanding of soil animal trophic ecology. In the following we summarize the main findings of these studies.

3.1. Food web structure

Overall, the stable isotope measurements of 292 oribatid mite species from our meta-study and their subsequent aggregation in trophic groups indicate that oribatid mites comprise six trophic groups, i.e., (1) primary decomposers, (2) fungal feeders/secondary decomposers, (3) predators/scavengers, (4) lichen feeders, (5) moss/plant feeders and (6) species that feed on marine algae (Fig. 1). Primary decomposers are animals that feed on fresh or little decomposed litter material little colonized by microorganisms and predominantly assimilate plant material, whereas secondary decomposers are feeding on dead organic matter heavily colonized by microorganisms or directly on microorganisms. However, rather than forming distinct trophic groups, there is a continuum between both (Scheu and Falca 2000). These findings are generally in agreement with ^{13}C and ^{15}N distribution patterns in soil food webs given in the literature survey of Adl et al. (2020). Additionally, there is one group characterized by high ^{13}C values, which is not a trophic group on its own since its high ^{13}C values result from the incorporation of inorganic carbon for hardening the cuticle (for defence purposes). It includes Phthiracaridae and Euphthiracaridae, but in part also species of the taxa Carabodidae and Liacaridae. It has been shown that the high ^{13}C signature originates from the incorporation of calcium carbonate; adding acid prior to stable isotope analysis shifts their ^{13}C values to one of the other six trophic groups (Pollierer et al., 2009; Maraun et al., 2011), with most of them grouping with fungal feeders/secondary decomposers. In the review of Maraun et al. (2011) the group was named "endophagous taxa" since the juveniles of many of the species of the group live inside needles or leaves (Norton and Behan Pelletier, 1991). However, since this does not uniformly apply, the group may better be named "taxa with mineralized cuticle" and this is what we adopt here.

The number of trophic groups as proposed in our current analysis (six plus the group with mineralized cuticle; see Fig. 1 for a schematic overview of oribatid mite trophic positions and Fig. 2 for details of ^{15}N and ^{13}C signatures) is higher than that in our previous review (Maraun et al., 2011), where we ascribed oribatid mite species to four trophic levels, i.e. predators/scavengers, fungal feeders/secondary decomposers, primary decomposers and lichen feeders, as well as a group with mineralized cuticle. The two additional trophic groups identified in this study comprise plant/moss feeders and marine algal feeders both of them comprising only few species. Since our current analysis covered a broad range of taxa as well as a very broad range of isotopic signatures, the number of trophic groups of oribatid mites is unlikely to increase in

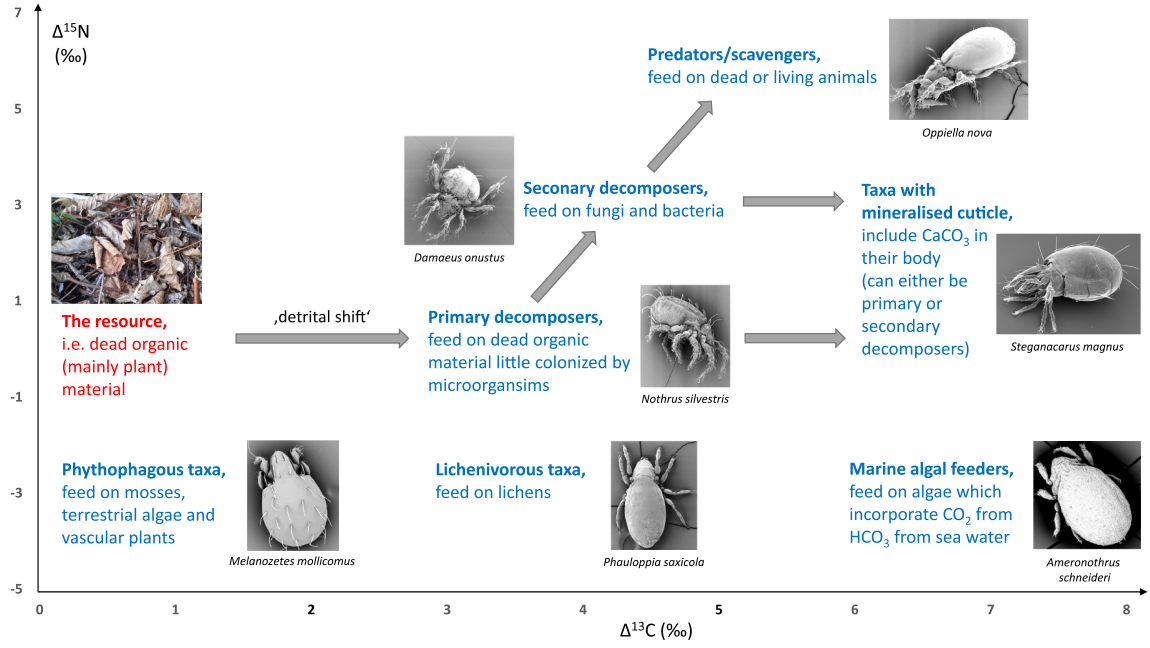

Fig. 1. Conceptual diagram of ^{15}N and ^{13}C enrichment (indicated by arrows) and oribatid mite trophic positions in the soil food web. Dead organic material is used as basal resource. Phytophagous taxa, lichen feeders and marine algal feeders are not connected with arrows with the dead organic material since they consume different resources. 'Detrital shift' means that primary decomposer taxa are not enriched in ^{15}N but strongly in ^{13}C which is probably due to the consumption of only certain parts of dead organic material by the oribatid mites.

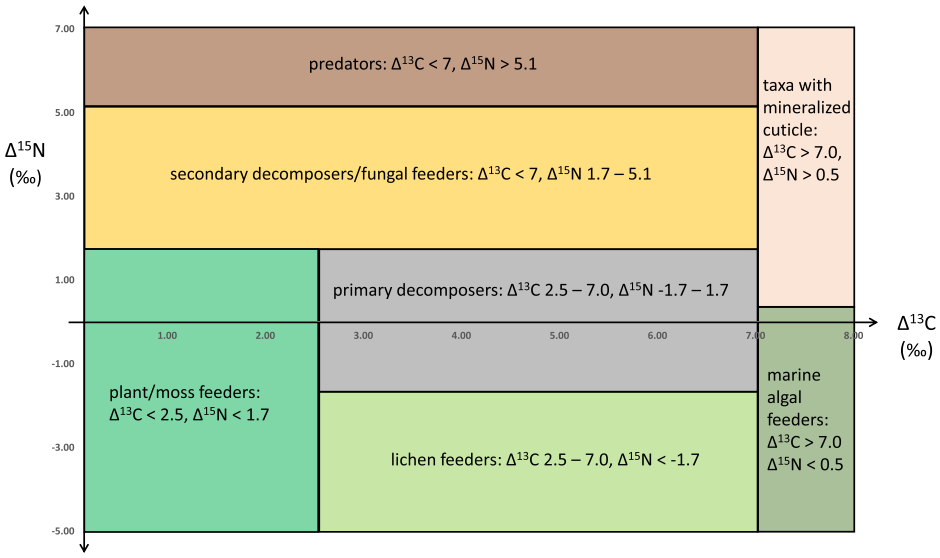

Fig. 2. Schematic assignment of (putative) soil animal taxa to six trophic groups, plus one group that incorporates $CaCO_3$. The grouping was conducted on the basis of the enrichment in $\delta^{15}N$ of 3.4 delta units per trophic level. For primary decomposer taxa, the grouping was set 1.7 higher and 1.7 lower than the baseline (=litter). Axis labels represent Δ values, i.e. stand for the (litter) calibrated values (if calibration was not possible, e.g. due to a lack of the baseline, we calibrated the datasets to a species from another dataset; for details see Table 1 in the Appendix). The division of the groups due to $\delta^{13}C$ was done in accordance with the potential food resource (e.g., mosses, lichens, marine algae) or the prior knowledge of the incorporation of $CaCO_3$ in their cuticle (Norton and Behan-Pelletier, 1991).

future studies. However, the adoption of novel methods such as compound specific lipid and amino acid analysis is likely to deepen our understanding of trophic niche differentiation in oribatid mites, especially between the groups we have identified, given that the separation between groups is not discrete but mostly a continuum, but also within the groups. Importantly, the variety of trophic niches of oribatid mites repeatedly evolved convergently (Schaefer and Caruso, 2019) indicating that nutritional strategies and trophic niches in oribatid mites are remarkably flexible. This strikingly contrasts the otherwise very uniform nutrition of non-Acari chelicerates as predators. A detailed mapping of the trophic ecology on the phylogeny of oribatid mites is needed for understanding the multiple dietary shifts in oribatid mites.

Stable isotope studies of other diverse soil arthropod taxa such as collembolans indicate that they also comprise a wide range of trophic groups spanning three to four trophic levels including primary decomposers, secondary decomposers/fungal feeders, predators/scavengers as well as herbivores (Chahartaghi et al., 2005; Potapov et al., 2016). Similarly, predatory taxa such as gamasid mites span across three trophic levels (Klarner et al., 2013), which implies that they feed on primary and secondary decomposers as well as other predators thereby functioning as intraguild predators. Remarkably, stable isotope analysis has also been applied to free-living soil nematodes (Kudrin et al., 2015; Melody et al., 2016), with the results reflecting the wide range of feeding types including microbivores and predators, similar to soil meso- and macrofauna. Eventually, Crotty et al. (2012) emphasized the importance of including protists in soil food web analyses using stable isotopes.

A number of factors have been assumed to affect the length of food chains in animal communities. The energy hypothesis (or resource availability hypothesis) assumes that paucity of basal resources may result in short food chains (Hutchinson, 1959; Thompson and Townsend, 2005). Conform to these assumptions only three trophic levels have been found in oribatid mites in resource poor habitats, such as mountain scree or fungal sporocarps, due to predatory taxa being rare or missing (Nae et al., 2021; Maraun et al., 2014). However, the generality of the energy hypothesis is disputed as other studies did not find the length of trophic chains to be related to the available energy, e.g. Post et al. (2000) did not find longer food chains in lakes with higher productivity.

Furthermore, it has been postulated that animal communities in tropical ecosystems are longer than in high latitude ecosystems (Reagan et al., 1996). Contrasting these assumptions, stable isotope studies of temperate and tropical oribatid mite communities indicate that they in fact span a similar range of trophic levels (Illig et al., 2005; Krause et al., 2019, 2021; Tsurikov et al., 2019). Presumably, food chains in tropical ecosystems are not longer compared to temperate ones potentially due to lower efficiency in the transfer of energy to higher trophic levels due to increased metabolic costs at high temperature (Meehan, 2006; Rall et al., 2012).

3.2. Trophic groups

Surprisingly few species of oribatid mites from temperate forests were ascribed to primary decomposers according to their ^{15}N and ^{13}C signatures which agrees with Maraun et al. (2011). Only taxa such as *Platynothrus peltifer*, *Nothrus palustris*, *Achipteria coleoptrata*, *Tectocepheus* spp. and some *Parachipteria* and *Camisia* species were assumed to live as primary decomposers. Freshly fallen litter material likely is recalcitrant und unpalatable since on one hand it includes substrates that can hardly be digested, such as lignin and cellulose, whereas on the other hand it includes substances that makes them hard to ingest (waxes) and hard to assimilate (e.g., tannins, polyphenols; Swift et al., 1979). Therefore, only few animal taxa live on such fresh plant litter material, whereas most species wait for microorganisms to colonize litter material after litter fall and make it more palatable after the breakdown of litter compounds difficult to digest or being toxic (Potapov et al., 2022). This is supported by the observation that in tropical ecosystems even less species may function as primary decomposers; Illig et al. (2005) only identified a single oribatid mite species in a study in the tropical Andes of Ecuador, and Krause et al. (2021) only found few primary decomposer species in lowland rainforest and plantations in Sumatra, Indonesia. In the tropics, from the viewpoint of a decomposer, litter quality is even lower than in temperate regions (Coq et al., 2010; Butenschoen et al., 2014; Marian et al., 2017) and this may explain the low number of taxa able to live on such resources.

Surprisingly, many species of oribatid mites neither were ascribed to decomposers nor to predators, but rather to lichen or moss feeders. Lichen feeders, such as *Cymberemaeus cymba*, *Phauloppia* spp., *Carabodes labyrinthicus* and *Mycobates* spp. (Norton and Behan-Pelletier, 2009), can easily be separated from all other taxa by having low ^{15}N and high ^{13}C signatures (Maraun et al., 2011). By contrast, mosses are characterized by ^{15}N and ^{13}C signatures close to those of vascular C3 plants, which also separates plant/moss feeders from other trophic groups. According to their stable isotope signatures, species such as *Melanozetes mollicomus*, *Minunthozetes semirufus* and *Edwardzetes edwardsi* likely feed on mosses or plant material (Bluhm et al., 2015; Maaβ et al., 2015). This is supported by the observation that *M. semirufus* burrows in stems of grasses

(Evans et al., 1961), and *M. mollicomus* and *E. edwardsi* typically are found associated with mosses (Materna, 2000; Erdmann et al., 2007; Norton and Behan-Pelletier, 2009; Smrz, 2010).

High ^{15}N signatures in a range of taxa of oribatid mites including Oppiidae, Suctobelbidae, *Hypochthonius rufulus* as well as some Damaeidae, Scheloribatidae and Galumnidae indicate that they live as predators or scavengers. Considering that oribatid mites for long have been assumed to live as decomposers this is rather surprising. However, even some early studies (Riha, 1951) as well as later experiments in laboratory (Heidemann et al., 2011, 2014a) pointed towards a number of oribatid mite taxa to live as predators or scavengers, with nematodes likely forming the dominant prey (Heidemann et al., 2014b).

Many soil animal taxa, including oribatid mites, include $CaCO_3$ into their cuticle – mainly for defensive purposes (Norton and Behan-Pelletier, 1991; Pachl et al., 2012). Since the formation of $CaCO_3$ is associated with strong ^{13}C fractionation, as reflected e.g., by the fact that fossil limestone (Vienna Pee Dee belemnite) is used as zero baseline for ^{13}C measurements, the incorporation of $CaCO_3$ into the cuticle of animals is associated with a strong shift in ^{13}C stable isotope signatures (Maraun et al., 2011; see above).

^{13}C was not only enriched in taxa incorporating minerals into their cuticle, but also in taxa that likely feed on marine algae, such as *Ameronothrus schneideri*, *Zachvatkinibates quadrivertex* and *Hermannia pulchella* (Haynert et al., 2017). The reason for their shift in ^{13}C signatures may resemble that of oribatid mites incorporating carbonates into their cuticle as many marine algae acquire CO_2 for photosynthesis in part from HCO_3 from the water column. Since HCO_3 has a ^{13}C signature of about −1.8‰ (Maberly et al., 1992), the incorporation of CO_2 from this source increases the ^{13}C signature of algae and thereby of algal consumers.

3.3. Trophic diversity

Ascribing oribatid mite species to trophic groups based on stable isotope values typically is straightforward as stable isotope values normalized to basal resources such as litter vary little among habitats (Scheu and Falca, 2000; Schneider et al., 2004). Recently, Lu et al. (2022) showed that stable isotope values of oribatid mite species also vary little with soil depth although stable isotope values of litter and soil organic matter increase in a consistent way with soil depth. The results indicate that trophic niches of oribatid mite species are remarkably constant. However, in certain species of oribatid mites stable isotope values also have been shown to vary among habitats and studies (see below), and, contrasting oribatid mites, Potapov et al. (2019a) found an increase in ^{15}N values in collembolans with soil depth.

When compiling stable isotope values of oribatid mite species for the present study we averaged $\Delta^{15}N$ and $\Delta^{13}C$ values, i.e. ^{15}N and ^{13}C values calibrated to litter, and ascribed species to trophic groups (Appendix, Table 2). Most of the 292 species for which data on stable isotopes have been published were ascribed to fungal feeders/secondary decomposers (43.7%), less to primary decomposers (27.0%) and predators (15.7%), and only few to those incorporating minerals into their cuticle (6.1%), feeding on lichens (4.9%), mosses (2.1%) or marine algae (0.7%). Overall, these findings support the view that the common ancestor of oribatid mites fed on fungi. This is further supported by the fact that many species of old taxa of oribatid mites including Crotonioidea and Euphthiracaridae feed on fungi, whereas moss feeders (e.g., *Melanozetes mollicomus*), lichen feeders (e.g., *Carabodes labyrinthicus*) and predatory species (e.g., Oppiidae and Damaeidae) comprise more derived taxa. However, these assumptions need rigorous statistical testing considering phylogenetic relationships among taxa.

Oribatid mites often are aggregated into a single trophic group in ecological studies (i.e., decomposers; Murvanidze and Kvavadze, 2010; Moore and de Ruiter, 2012), which ignores their trophic diversity. In temperate forest ecosystems, this might be justified as oribatid mite species in these ecosystems in fact may predominantly feed on fungi and function as secondary decomposers (Pollierer and Scheu, 2021). However, in tropical and subtropical regions the fraction of predators may be high and primary decomposers may be lacking almost entirely (Illig et al., 2005; Krause et al., 2019).

3.4. Trophic plasticity

Trophic plasticity plays an important role for colonizing habitats where environmental conditions vary in time. Thereby, trophic plasticity may also help to cope with global changes as trophically plastic species may suffer less from climate and temperatures changes (Ingels et al., 2012). For investigating oribatid mite trophic plasticity, we compared the variability in stable isotope data of species among sites. Of the 292 taxa included in this study, stable isotope data of 110 taxa were measured at more than one site (Appendix, Table 3). Of the 53 taxa that were measured in two habitats 40% (=21 taxa) were ascribed to the same trophic group, whereas 60% (=32 taxa) were ascribed to different trophic groups. Similarly, of the 25 taxa that were measured in three habitats 32% (=7 taxa) were ascribed to the same trophic group, whereas 68% (=15 taxa) to two or three different trophic groups. Similar figures applied to taxa that were measured four or more times; of the 13 species that were measured four times 38% (=5 taxa) were ascribed to the same trophic group and 62% (=8 taxa) to two or more trophic groups (for details see Appendix, Table 3). Overall, these figures suggest that about one-third of the oribatid mite species are trophically consistent across habitats, whereas about two-thirds are trophically plastic and able to change their trophic level between habitats. This indicates that the majority of oribatid mite species shows a remarkable flexibility in the diet they are using and thereby may respond in a flexible way to environmental changes (Gan et al., 2014). However, in the great majority of oribatid mite species variations in the tropic level were limited to two adjacent levels, only in very few species the trophic level they were ascribed to varied for more than two trophic levels. Among those were *Tectocepheus sarekensis, Eniochthonius minutissimus* and *Nanhermannia nana,* which varied across three or even more trophic levels among habitats. Interestingly, these taxa are very widespread and reproduce via parthenogenesis which supports the view that parthenogenetic oribatid mite species may be more generalistic than sexual species by possessing a general purpose genotype (Lynch, 1984; Maraun et al., 2022). However, in other parthenogenetic species, such as *Platynothrus peltifer*, *Hypochthonius rufulus* and *Nothrus palustris*, the trophic position they were ascribed to varied little between habitats indicating trophic consistency, and suggesting that the relationship between reproductive mode and trophic plasticity deserves further attention.

Contrasting our findings, Gan et al. (2014) found trophic plasticity in oribatid mites to be low and Lu et al. (2022) also found the trophic position of oribatid mites to be surprisingly constant irrespective of forest type. On the other hand, Krause et al. (2021) showed the stable isotope niche of a number of tropical oribatid mite species to vary between habitats, however, the niche shifts were rather low in respect to ^{15}N values and more pronounced in ^{13}C values indicating that shifts in trophic niches of oribatid mites are mainly due to shifts in the use of basal resources rather than trophic levels. Overall, results of the data we compiled and the study of Krause et al. (2021) indicate that trophic plasticity of oribatid mite species may has been underestimated. Possibly, trophic flexibility of oribatid mites is higher in the tropics than in temperate regions. Resolving these questions needs further studies including a large number of replicates of stable isotope measurements of single individuals per species within but also across habitats. With recent advances in stable isotope methodology this now can be achieved (Crotty et al., 2013; Langel and Dyckmans, 2014). Overall, studying trophic plasticity of oribatid mite species as varying with reproductive mode, position in the food web, body size and other traits is a promising and exciting topic for future research.

3.5. Taxonomic resolution

According to the data compiled for this review 59.6 and 69.4% of the variance in ^{13}C and ^{15}N data of oribatid mites could be explained at the level of species, respectively. When analysing the data on genus, family, superfamily and suborder level the explained variance declined for both ^{15}N and ^{13}C (Fig. 3). Eventually, when aggregating the data on suborder level, the explained variation declined to 15.5 and 5.5% for ^{15}N and ^{13}C, respectively.

The strong decline with coarser taxonomic resolution reflects that species from the same taxonomic group, e.g. from the same genus, often occupy very different trophic positions. For example, *Carabodes labyrinthicus* lives as a decomposer/lichen feeder, whereas *Carabodes reticulatus* lives as fungal feeder. Similarly, *Oribatella calcarata* has been classified as fungal feeder, *O. longispina* as primary decomposer and *O. quadricornuta* as fungal feeder, which also may consume mosses, i.e. lives as herbivore (Nae et al., 2021). Furthermore, *Nothrus palustris* lives as primary decomposer, whereas *N. sylvestris* as fungal feeder/secondary decomposer and potentially in part even as predator/scavenger. These results support the conclusions of Schaefer and Caruso (2019) on the lack of phylogenetic signal in the trophic position of oribatid mites reflecting that shifts in the diet occurred multiple times convergently in terminal lineages. This argues for the necessity to analyse oribatid mite communities at high taxonomic resolution if we are to investigate their trophic niches and relationships with food resources.

The lack of phylogenetic signal in trophic niches of oribatid mites, however, may not uniformly apply as certain groups at the level of e.g., superfamilies are characterized by similar stable isotope signatures (Fig. 4). For example, Oppioidea, Hypochthonioidea and Damaeoidea occupy high trophic positions, and this applies to most species of these taxa. High ^{13}C signatures in Phthiracaroidea, Euphthiracaroidea and Carabodidae also apply to most of the species in these taxa suggesting that defence mechanisms based on the incorporation of $CaCO_3$ into their cuticle are an ancient trait which evolved in common ancestors of each of these lineages. Low ^{15}N signatures in Neoliodoidea, Licneremaoidea, Hermannioidea and Achipteroidea may indicate that living as primary decomposer is an ancestral trait in these taxa. Similarly, analysing stable isotope data at family level, Tsurikov et al. (2019) found Oppiidea, Scheloribatidae, Galumnidae and Damaeidae to occupy high trophic level positions, and Carabodidae, Phthiracaridae, Liacaridae and Galumnidae (among others) to possess mineralized cuticles.

One shortcoming of the present review is that it is based predominantly on data from temperate and boreal ecosystems; there are only few studies on stable isotopes of oribatid mites from tropical regions (Ecuador: Illig et al., 2005, Indonesia: Krause et al., 2019, 2021; Kenia: Lagerlöf et al., 2017; Vietnam: Tsurikov et al., 2019). The few data existing, however, suggest that the conclusions drawn above also hold for oribatid mites from tropical regions, although they often have been only analysed at family level (Lagerlöf et al., 2017; Tsurikov et al., 2019). Overall, the data available indicate that oribatid mites of tropical and temperate regions occupy a similar range of trophic niches, but primary decomposers may be less common in the tropics (Illig et al., 2005). The scarcity of stable isotope data at species level from the tropics, among other reasons, presumably reflects the lack of a suitable determination keys for tropical regions and the fact that many oribatid mites from tropical regions have not been described taxonomically yet. The findings of Krause et al. (2019, 2021) on trophic niches of oribatid mites in different land-use systems in Sumatra, Indonesia, however, indicate that for understanding shifts in trophic niches with changes in land use needs species level analyses.

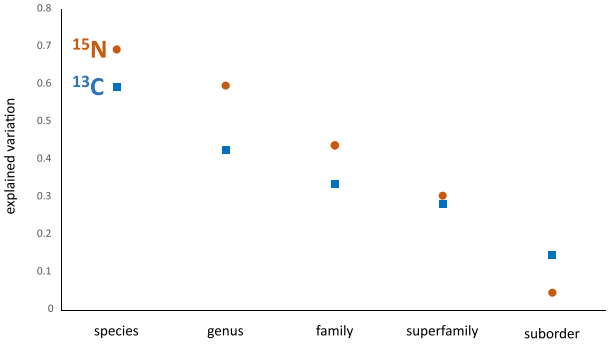

Fig. 3. Explained variation in $\delta^{15}N$ and $\delta^{13}C$ data when analysed on species, genus, family, superfamily and suborder level (grouping on the basis of Subias, 2020) indicating the loss of information when aggregating oribatid mite species on higher taxonomic level. Explained variation was estimated by marginal R^2 based on linear mixed-effect models including taxonomic level as fixed effects (for details see the R script in the Dryad Digital Repository).

3.6. Stable isotopes, morphology and reproductive mode

The trophic ecology of oribatid mites may be correlated with morphological and other traits, i.e. predatory taxa may have smaller chelicera for picking up nematodes, whereas primary decomposers may have more compact and stronger mouthparts for cracking organic material. In fact, it has been shown that the morphology of mouthparts, especially the leverage of the chelicerae, changes from predators to secondary decomposer to primary decomposers; and this change is correlated with stable isotope signatures (Perdomo et al., 2012). This indicates that primary decomposers indeed need more power for chewing up litter materials, whereas predators do not need much leverage, but just have to be fast in catching their prey. Including a wider range of traits into such studies is an exciting field of future research. Correlations between other traits of oribatid mites, e.g. body size, ontogenetic stage or reproductive mode, with their trophic ecology (indicated by ^{15}N and ^{13}C signatures) may allow more detailed understanding of the factors and constraints shaping oribatid mite evolution.

Exploring correlations between stable isotopes and reproductive mode may be particularly interesting as it may allow deeper insight into the multiple transitions from sexual to parthenogenetic reproduction in oribatid mites (Schaefer et al., 2010; Pachl et al., 2021). For example, the transition might have been more frequent in primary decomposers since they do not interact with living resources, i.e. “detritus … that does not exactly bite back” (Hamilton, 1996; Scheu and Drossel, 2007), whereas species higher in the food web may be bound to reproduce sexually to keep in pace with the evolution of their prey. Preliminary studies in this direction, however, indicate that the patterns are not clear cut (Schaefer and Caruso, 2019). Including taxa which (putatively) re-evolved sex from parthenogenetic ancestors may as well be interesting since the transition to sex has been proposed to be related to changes in resource use (Domes et al., 2007).

4. Limitations of stable isotope-based trophic ecology

Despite the fundamental progress and exciting findings on the trophic ecology of soil animal species and communities that emerged from stable isotope studies there also are limitations of the method. Channelling of basal resources through the soil food web cannot be traced, i.e. it is impossible to separate bacterial feeding from fungal feeding as well as feeding on different taxa of microorganisms. Further, the method typically does not allow to identify links between predator and prey taxa. Also, omnivory is difficult to detect since stable isotope signatures integrate across prey species of similar but potentially also very different trophic position. These problems may be overcome by using more sophisticated techniques such as fatty acid, amino acid or molecular gut content analyses (Traugott et al., 2013; Heidemann et al., 2014 a,b; Maraun et al., 2020; Pollierer and Scheu, 2021; Potapov et al., 2022).

Fatty acid analysis allows separation of trophic channels in soil food webs e.g., by separating feeding on algae, plants, bacteria, fungi and animals (Menzel et al., 2018; Kühn et al., 2020, 2021; Maraun et al.,

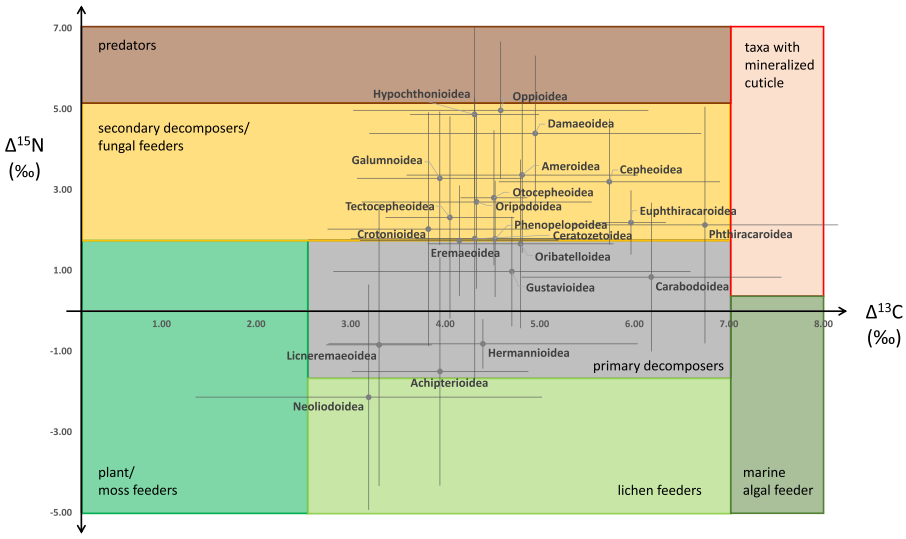

Fig. 4. Assignment of oribatid mite families to six trophic groups, plus one group that incorporates $CaCO_3$. The grouping was conducted on the basis of the enrichment in $\delta^{15}N$ of 3.4 delta units per trophic level. For primary decomposer taxa, the grouping was set 1.7 higher and 1.7 lower than the baseline (=litter). Axis labels represent Δ values, i.e. stand for the (litter) calibrated values. The division of the group due to $\delta^{13}C$ was done in accordance with the potential food resource (e.g., mosses, lichens, marine algae) or the prior knowledge of the incorporation of $CaCO_3$ in their cuticle (Norton and Behan-Pelletier, 1991). Note that oribatid mite species - when aggregated on family level - only range over three trophic groups.

2020; Twining et al., 2020). However, the method does not allow to quantify the relative importance of the different channels, but this may be achieved in future (Kühn et al., 2020, 2021). Additionally, feeding on saprotrophic and mycorrhizal fungi cannot be separated.

Amino acid analysis allows progress in some of these issues. For example, it has been shown recently that feeding on saprotrophic and mycorrhizal fungi might be separated (Pollierer et al., 2020) and first results indicate that in soil microarthropods of temperate forests feeding on mycorrhizal fungi is of limited importance (Pollierer and Scheu, 2021). Amino acid analyses also revealed that earthworms and enchytraeids rely on plants or bacteria as their primary source of essential amino acids but not on fungi (Larsen et al., 2016), and that earthworms act as competitors but also as consumers of microorganisms in soil food webs (Potapov et al., 2019b). Wide application of the method to microarthropods such as oribatid mites, however, is restricted by the fact that rather large amounts of tissue is needed for the analyses.

Molecular gut content analysis is an additional tool for deeper understanding of trophic interactions in soil food webs. Contrasting the biochemical techniques described above it allows to detect the food material ingested at the level of species and thereby to identify links between consumer and prey species in soil food webs. However, it has the disadvantages that only recently ingested food can be detected and that ingested food is not necessarily the one which is assimilated (Lavelle et al., 2001). Further, quantification of the relative contributions of different species/taxa to the diet of consumers remains a challenge. Until today, only few studies used molecular gut content analysis for understanding trophic links between oribatid mites and their diet in soil food webs. Using a meta-barcoding approach Gong et al. (2018) investigated the microbial communities in seven species of oribatid mites of different trophic levels from temperate forest ecosystems. The results indicated that bacteria in the gut include commensals or mutualists, which may foster the digestion process and which may have coevolved with the host. By contrast, fungal communities in the gut correlated with the trophic niche of the host indicating that fungi served as food resource for the studied oribatid mite species.

Molecular gut content analyses may employ specific primers designed to amplify the DNA of specific prey taxa in the gut of consumers such as nematodes or certain nematode taxa ("diagnostic PCR"; Heidemann et al., 2011, 2014a). However, also general primers might be used targeting e.g., bacteria or fungi (next-generation sequencing; NGS) as in the study of Gong et al. (2018). Both methods have advantages and disadvantages (Traugott et al., 2013; Rennstam Rubbmark et al., 2019). Diagnostic PCR may allow more reliable detection of the targeted taxa in the gut of consumers, but detection depends on a number of factors including time elapsed since ingestion, amount of prey ingested and primer specificity. Further, for quantifying the importance of prey taxa for consumer nutrition a large number of individual consumers needs to be investigated. NGS targeting a wide range of species/taxa ingested may be less reliable than diagnostic PCR in detecting certain prey taxa/species; and quantification of individual prey taxa/species is difficult due to primer bias, i.e. selective amplification of DNA of certain species/taxa.

Despite existing shortcomings, molecular gut content analysis may help in elucidating what predatory/scavenging oribatid mite taxa such as Oppiidae, Scheloribatidae and Damaeidae, are really feeding on. Since oribatid mites are slow mowing, they are likely to prey predominantly on stationary or slow moving prey such as nematodes, enchytraeids, eggs of other invertebrates or carcasses of other animals (Heidemann et al., 2011, 2014 a,b), but this needs further investigation. Also, the role of protozoans in the diet of oribatids needs further attention in particular in aquatic taxa such as *Limnozetes* and *Hydrozetes*, also characterized by high ^{15}N signatures indicating that they may graze on protists/periphyton colonizing the aquatic plants they live on (Lehmitz and Maraun, 2016). Molecular gut content analysis may also resolve if oribatid mite species with a stable isotope signal pointing to plant feeding, in fact feed on plant material or on algae. Overall, the limitations of stable isotope-based studies on trophic relationships in oribatid mites call for more sophisticated methods allowing more complete understanding of trophic links of oribatid mites and their integration into soil food webs.

5. Perspectives for future stable isotope studies

To better understand the structure of soil animal communities and their trophic interactions more information is needed on the degree of generalism of soil animal species. Widespread generalist feeding results in exceptionally complex food webs with high link density as is typical for soil food webs (Digel et al., 2014), and generalist feeding including trophic level omnivory are key characteristics driving the diversity and stability of food webs (Neutel et al., 2007; Gellner and McCann, 2012). Identifying the manifold links of generalist feeders is a challenge and will only be possible by including the full complement of methods available, in particular molecular gut content analysis. Although being assumed to be very widespread across taxa in soil animal communities (Scheu and Setälä, 2002; Digel et al., 2014; Erktan et al., 2020), we still know little on the degree of generalism in soil animal food webs (Potapov et al., 2022). For this review, the level of generalism in oribatid mite species and their degree of trophic plasticity could only indirectly

be assessed by investigating how often they were ascribed to different trophic groups (when measured in more than one habitat). This is due to the fact that in most studies investigating stable isotopes in oribatid mites individuals were pooled, limiting the investigation of variations in trophic niches within species. However, with technological advances stable isotope signatures can now be measured at the level of individual oribatid mites as done in Krause et al. (2021), and this needs to be adopted more widely in the future. Knowledge on trophic plasticity is particularly important to allow predictions on how soil animal communities may respond to global climate changes (Gan et al., 2014). Analysing stable isotope signatures at the level of individuals may also help in resolving long-standing evolutionary questions such as if parthenogenetic oribatid mites possess a widely adapted general purpose genotype (Lynch, 1984) or occupy narrow trophic niche conform to the frozen niche variation hypothesis (Vrijenhoek, 1979, 1984). Clarifying these questions is essential to understand why parthenogenetic reproduction is exceptionally high in oribatid mites. Further, studying trophic niche breadth at the level of individuals may allow to investigate if the width of niches varies with trophic level. Taxa low in the food web such as decomposers feed on a mixture of resources including dead organic material, bacteria, fungi and protozoans, and may therefore have a broader trophic niche compared to species high in the food web living as predators.

Moreover, changes in the trophic niche of oribatid mite species during ontogeny need closer attention and have been little studied using stable isotopes (Crotty and Adl, 2019). Potentially, as in holometabolous insects, oribatid mites may switch diets between juveniles and adults to avoid competition which may contribute to the high density of oribatid mites in particular at high latitude ecosystems. However, the few studies existing which investigated both juveniles and adult oribatid mites suggest that trophic niches vary little between juveniles and adults and differ little even in phthiracarid oribatid mites where juveniles live inside of needles and adults forage freely in litter indicating that trophic niches change little during ontogeny (Schneider et al., 2004). However, more studies on trophic niches of juvenile and adult oribatid mites are needed.

One important aspect of the trophic ecology of oribatid mites which also received little attention until today is the temporal variability of trophic niches. Information on temporal variability is important for understanding the high predictability of the composition and density of oribatid mites in soil despite their long life cycles (Maraun and Scheu, 2000). Temporal variability in trophic niches may also help understanding differences in oribatid mite communities of stable habitats such as tropical forests compared to habits exposed to strong seasonal dynamics such as temperate and boreal forests or habitats experiencing strong and frequent abiotic fluctuations such as salt marshes. Finally, most studies on the trophic ecology of oribatid mites using stable isotopes are from boreal and temperate regions in Europe, only few studies are from tropical regions and regions outside of Europe (Illig et al., 2005; Krause et al., 2019, 2021; Lagerlöf et al., 2017; Tsurikov et al., 2019; Perdomo et al., 2012) or from Antarctica (Bokhorst et al., 2007). From most other continents studies are either lacking entirely (North America) or only single studies covering only few species are available as is the case for Africa (but see Lagerlöf et al., 2017), Australia (but see Perdomo et al., 2012) and Asia (but see Krause et al., 2019, 2021). Similarly, most studies investigated oribatid mites from forest ecosystems, studies from other habitats, such as grasslands, peat bogs, tundra and Mediterranean sites as well as from aquatic habitats, are scarce (but see Maaβ et al., 2015; Lehmitz and Maraun, 2016). Also, microhabitats such as dead wood, rhizosphere and suspended soils received little attention (but see Bluhm et al., 2015). Therefore, although being used for more than 20 years, there still are ample opportunities for extending our knowledge on the trophic ecology of oribatid mites using stable isotopes.

6. Conclusions, outlook and perspectives

Overall, the analysis of stable isotopes in soil microarthropods, and in particular in oribatid mites, has changed our view on the trophic structure of and trophic niches in soil animal communities. After treating complex groups such as oribatid mites as a single trophic group, usually as primary or secondary decomposers (Luxton, 1972; Harding and Stuttart, 1974) or as panphytophages (Behan and Hill, 1978; Hunt et al., 1987), the diversity of trophic niches and range of trophic positions they occupy now is firmly established. Stable isotopes therefore contributed significantly to overcome the situation described by Hunt et al. (1987) that "there are simply too many species and there is too little known about the diets and physiology of many species to describe detrital webs at the species level"; and we now can build soil animal food webs closely resembling the real world rather than representing caricatures of nature (Polis, 1991, 1994). Therefore, stable isotope analyses opened new perspectives on soil microarthropod ecology. Its implications are now well covered in recent textbooks (Nielsen, 2019) and review articles (Potapov, 2022; Potapov et al., 2022), and will form the basis for studies on the trophic structure and functioning of soil animal communities for decades. However, still a wide range of topics await further elucidation, but may now be approached using more sophisticated techniques such as fatty acid, amino acid and molecular gut content analysis. However, even with the full set of methodical tools now available disentangling the structure and functioning of soil food webs in a realistic way remains a challenge and requires investigations including a wide range of different types of ecosystems and habitats from the arctic to the tropics.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available from the Dryad Digital Repository (doi.org/10.5061/dryad.bcc2fqzgj).

Acknowledgements

We gratefully acknowledge support by the Open Access Publication Funds of the University Göttingen. We thank Christian Bluhm for providing *Melanozetes mollicomus* specimens for SEM pictures.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108890.

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