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Review

Stable isotopes revisited: Their use and limits for oribatid mite trophic ecology

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ABSTRACT

In this review we summarize our knowledge of using stable isotopes ($^{15}N/^{14}N$, $^{13}C/^{12}C$) to better understand the trophic ecology of oribatid mites. Our aims are (a) to recapitulate the history of stable isotope research in soil animals with a focus on oribatid mites, (b) to present new stable isotope data for oribatid mites and overview the current state of knowledge of oribatid mite trophic niche differentiation, (c) to compile problems and limitations of stable isotope based analyses of trophic relationships and (d) to suggest future challenges, questions and problems that may be solved using stable isotope analyses and other novel techniques for improving our understanding on the trophic ecology of soil invertebrates. We conclude that (1) in addition to $^{15}N/^{14}N$ ratios, $^{13}C/^{12}C$ ratios contribute to our understanding of the trophic ecology of oribatid mites, allowing, e.g. separation of lichen- and moss-feeding species, (2) there likely are many lichen but few moss feeding oribatid mite species, (3) oribatid mite species that are endophagous as juveniles are separated by their stable isotope signatures from all other oribatid mite species, (4) fungivorous oribatid mite species cannot be separated further, e.g. the fungal taxa they feed on cannot be delineated. A particular problem in using stable isotope data is the difficulty in determining signatures for basal food resources, since decomposing material, fungi and lichens comprise various components differing in stable isotope signatures; $^{13}C/^{12}C$ ratios and potentially other isotopes may help in identifying the role of these resources for decomposer animal nutrition.

1. History of using stable isotopes in soil food web analysis

Terrestrial soil ecologists came rather late to the use of stable isotope ratios (mainly $^{15}N/^{14}N$ and $^{13}C/^{12}C$) to analyze the structure of food webs. When we started with our now frequently-cited study about stable isotope ratios ($^{15}N/^{14}N$) in soil-living oribatid mites (Schneider et al., 2004) in 2003, stable isotopes had been used for decades to study trophic relationships in marine (Minagawa and Wada, 1984; Sholto-Douglas et al., 1991) and freshwater systems (Gu et al., 1994; Hall, 1995). In soil systems the seminal papers by Ponsard and Arditi (2000) and Scheu and Falca (2000) used stable isotopes ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) for the first time to analyze the trophic structure of soil animal food webs in a comprehensive way. The results of these two studies indicated that food chains in soil are rather short, with decomposers being clearly separated from predators, but they suggested strong variation in the trophic position of species of both decomposers and predators.

Stable isotopes have been used not only to study trophic levels in food webs but also to investigate the trophic ecology of specific taxonomic groups, e.g. earthworms (Martin et al., 1992), seabirds (Hobson et al., 1994), pinnipeds (Hobson et al., 1997), amphibians (Altig et al., 2007) and lizards (Struck et al., 2002). Their application to soil animals started in the 1980s with the investigation of termites (Boutton et al., 1983; Tayasu, 1998) and was continued by studies on ants (Blüthgen et al., 2003) and earthworms (Schmidt and Ostle, 1999). The results indicated marked trophic niche separation of the respective species. It was not until 2004 that stable isotopes were used to delineate trophic niches of a major group of putatively saprophagous soil mesofauna, the oribatid mites (Schneider et al., 2004), and one year later this study was followed by a similar investigation of Collembola (Chahartaghi et al., 2005). A third study focusing on the predatory soil mesofauna, i.e. mesostigmata (gamasid) mites, is pending (B. Klarner, unpublished data).

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Only nine species of oribatid mites were included in the stable isotope study of Scheu and Falca (2000) and none in that of Ponsard and Arditi (2000). Therefore, in Schneider et al. (2004) we chose to investigate the stable isotope ratios ($^{15}N/^{14}N$) of oribatid mite species of forests in a comprehensive way, by including all major taxa and comparing different forests. Further, for investigating variations in stable isotope ratios between habitats and developmental stages we included oribatid mites from different microhabitats, e.g., the bark of trees, and analyzed both adults and juveniles of some species. For delineating the baseline, potential food resources of decomposer species were investigated.

The use of stable isotopes for studying food webs was introduced by DeNiro and Epstein (1981), Minagawa and Wada (1984) and Wada et al. (1991). They found that the trophic structure of animal communities can be evaluated by analyzing the natural variation in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios. On average, animal tissues are enriched in ^{15}N compared with their food source by about of 3.4 δ units per trophic level and in ^{13}C by about 1 δ unit (Post, 2002). This allows fast and standardized evaluation of the trophic structure of animal food webs even if little is known of predator–prey relationships. This is particularly advantageous for analyzing food web structure of cryptic communities like those in soil. Stable isotope analysis is particularly powerful in opening the structure of soil animal food webs if combined with other recently developed methods for analyzing food webs, such as fatty acid analysis (Chamberlain et al., 2004; Ruess et al., 2004, 2005a) and molecular gut content analysis (King et al., 2008), as these methods allow closer identification of trophic links. Similar to fatty acid analysis, but in contrast to molecular gut content analysis, stable isotope ratios of animal tissue reflect nutrition over long periods of time, allowing the delineation of general characteristics of the trophic structure of food webs. Further, variations in $^{13}C/^{12}C$ ratios of food resources, e.g. between C3 and C4 plants, allow to trace the transfer of carbon from major resources through animal food webs (Oelbermann et al., 2008; Pringle and Fox-Dobbs, 2008).

2. Uncovering the trophic structure of oribatid mite communities

The analysis of the stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) has contributed significantly to our understanding of the trophic structure of soil animal taxa and this started with the detailed analysis of oribatid mites (Schneider et al., 2004). First and most important, this study showed that stable isotope ratios of nitrogen in this single taxonomic group of soil invertebrates vary to an extent that was entirely unexpected. In fact, the results indicated that oribatid mites span about four trophic levels, similar to what had been suggested previously for the total invertebrate soil animal food web of deciduous forests (Scheu and Falca, 2000). This is highly incongruent with the common practice of lumping oribatid mites into a single trophic group and indicates that soil food webs based on such coarse taxonomic units lack realism and represent caricatures of nature.

Early studies based on physical gut content analyses and direct observation had already suggested that "mycophagous" soil invertebrates like oribatid mites in fact are trophically diverse and include species living as predators, scavengers, algal and lichen feeders (e.g. Walter, 1987), but the findings remained somewhat anecdotal and were largely ignored. Using stable isotope analysis and analyzing a wide range of oribatid mite species living in the same habitat, the study of Schneider et al. (2004) confirmed these observations and thereby received considerable attention. Based on oribatid mites sampled in different forests the study brought realism into previously scattered investigations of the feeding mode of decomposer soil mesofauna. Much previous knowledge derived from laboratory observations of species kept under artificial conditions and offered food materials without choice. For example, mites of the genus *Hypochthonius* were shown to consume fungi (Maraun et al., 1998) and algae (Norton and Behan-Pelletier, 2009), but also living and dead animals, i.e. they can function as predators or necrophages (Riha, 1951). High $^{15}N/^{14}N$ ratios of *Hypochthonius rufulus* in the study of Schneider et al. (2004) suggest that this species in fact predominantly lives on an animal diet, presumably nematodes or other small and slow moving soil invertebrates which these rather slow moving mites are able to catch, or on their dead remains. Similarly, stable isotope analyses support early assumptions of the diet of the bark-living species *Mycobates parmeliae*, which was named after lichens of the genus *Parmelia* in which it is often found. Lichens are characterized by very specific stable isotope signatures (low $^{15}N/^{14}N$ and high $^{13}C/^{12}C$ ratios), which separate lichens from most other food resources (Fischer et al., 2010); therefore, oribatid mite species with signatures close to the lichens in which they live are likely to also feed on them.

One of the remarkable findings of Schneider et al. (2004) was that a given oribatid mite species appears to occupy a very similar trophic niche even if living in rather different forests. Earlier findings based on stable isotope ratios suggested that trophic niches of soil invertebrates also differ little with soil depth (Scheu and Falca, 2000). Further, Schneider et al. (2004) found little difference between signatures of adult and juvenile oribatid mite species, suggesting that trophic niches change little during ontogeny. Overall, these results point to a remarkable constancy of trophic niches in oribatid mites and presumably also other soil mesofauna such as Collembola (Chahartaghi et al., 2005). Constancy and discreteness of trophic niches is particularly surprising considering the wide range of food materials which decomposer soil invertebrates, such as oribatid mites and Collembola, consume if offered in the laboratory (Ruess et al., 2005a). The similarity of a species' stable isotope signature in different habitats (calibrated to stable isotope ratios of the predominant litter material) and in different studies further indicates that trophic niches vary little over time. Temporal constancy also is surprising, as litter materials enter the decomposer system in a pulsed way – particularly in temperate forest ecosystems – and are colonized and broken down by a succession of different fungal species (Hudson, 1968; Hayes, 1979; Osono, 2007). However, detailed data on temporal changes in stable isotope signatures in soil animal species remains scarce, so general conclusions on changes in trophic niches in time and space are difficult to draw. Also, the conclusion that trophic niches of oribatid mite species change little during ontogeny may be premature and needs further investigation. Generally, little is known about differences in feeding habits between juveniles and adults in oribatid mites and other soil invertebrates; stable isotope analyses may be particularly helpful in elucidating if marked changes in morphology in phylogenetically derived species – such as brachypyline oribatid mites – are associated with shifts in diets.

Recent analyses of stable isotope signatures of bark-living oribatid mites (Erdmann et al., 2007) support the conclusion of Schneider et al. (2004) that individual species occupy distinct trophic niches. However, as with soil species, the exact food materials of bark-living species remain unclear; their stable isotope ratios do not match the signatures of potential food resources analyzed so far, indicating that they feed on cryptic resources, potentially algae or filamentous fungi that decompose bark residues. Surprisingly, we could not ascribe a single oribatid mite species to moss-feeding despite their collective common name, “moss mites”. Mosses are characterized by low $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios (Bokhorst et al., 2007; Fischer et al., 2010), which should allow identification of their consumers.