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Trophic diversity and niche partitioning in a species rich predator guild – Natural variations in stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of mesostigmatid mites (Acari, Mesostigmata) from Central European beech forests

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ABSTRACT

A large number of predatory mesostigmatid mite species populate forest soils in high densities. The present study investigates the trophic structure of the Mesostigmata community of old growth beech stands in Central Germany and identifies potential prey groups using natural variations in stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$). Data on relative abundances and body mass were included for each of the 40 species studied to analyze functional aspects in Mesostigmata feeding ecology. The results indicate that Mesostigmata predominantly feed on secondary decomposers, whereas primary decomposer and intraguild prey are of minor importance. Dominant species featured high $\delta^{13}C$ signatures suggesting that they predominantly feed on species relying on root derived resources such as bacterial feeding nematodes. Less abundant species where characterized by lower $\delta^{13}C$ values suggesting that they predominantly feed on prey relying on litter derived resources such as fungal feeding Collembola. Related taxa often had distinctively different isotope ratios suggesting that trophic niche partitioning facilitates coexistence of morphologically similar species. Unexpectedly, the trophic position of Mesostigmata species was not related to body size reflecting the varying trophic position of their main prey, nematodes and Collembola, suggesting that body size is a poor predictor of trophic position in soil food webs.

1. Introduction

Mesostigmatid mites (Acari, Mesostigmata) are the main predators in mesofauna food webs of temperate forest and agricultural soils (Ruf and Beck, 2005). In beech forests total biomass of Mesostigmata species, which typically are only few millimeters in length, is equivalent to that of predators such as centipedes (Chilopoda) and spiders (Araneida) with at least one magnitude larger body size (Schaefer, 1990; Scheu et al., 2003). In numbers Mesostigmata surpass other arthropod predators by far, reaching typically 4000–10,000 ind. m^{-2} (Schaefer, 1990; Ruf and Beck, 2005). Recent studies suggest that Mesostigmata are among the most effective predators in soil food webs; due to their high density they effectively control prey populations (Schneider et al., 2012).

Mesostigmata are diverse, about 1000 species are described for Central Europe (Karg, 1993) and often more than 30 species co-occur on a single square meter of soil (Heldt, 1995). Unfortunately, due to their small size Mesostigmata are rarely included in studies on trophic interactions in soil food webs. If included they usually are treated as a homogeneous functional group, ignoring species specific differences in prey spectra (Moore et al., 1988). Knowledge on the trophic ecology of Mesostigmata is primarily based on laboratory observations with only few species studied in detail. Feeding experiments indicate some specialization among Mesostigmata species, with preferences for prey with certain traits or taxonomic affiliation e.g., worm-like prey, microarthropods, Collembola or Nematoda (Karg, 1983, 1986, 1989b; Walter et al., 1988; Koehler, 1999; Prischmann et al., 2011). These preferences can be linked to morphological features of the chelicerae, though the prey type could not be predicted reliably from cheliceral morphology (Buryn and Brandl, 1992). Studies on feeding interactions of Mesostigmata in the field are missing entirely.

The analysis of stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) is a well established tool for investigating the trophic structure of soil animal food webs (Scheu and Falca, 2000; Tiunov, 2007). The concentration of the heavy nitrogen isotope ^{15}N increases from food sources to consumers and therefore isotope ratios of nitrogen can be used to ascribe species to trophic levels

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(DeNiro and Epstein, 1981; Peterson and Fry, 1987; Scheu, 2002). The enrichment of ^{15}N in consumers to some extent varies with diet, age, feeding type, excretion mode and taxonomic affiliation (Oelbermann and Scheu, 2002; Vanderklift and Ponsard, 2003; Haubert et al., 2005; Tiunov, 2007), however, the average enrichment by 3.4‰ as proposed by Post (2002) has been found to be a reliable figure also applying to soil animals including predators (Schneider et al., 2004; Chahartaghi et al., 2005; Oelbermann and Scheu, 2010). For detritivores the enrichment presumably is lower with an average of about 0.5‰ (Vanderklift and Ponsard, 2003; Oelbermann and Scheu, 2010). In contrast to ^{15}N, concentrations of ^{13}C change little from diet to consumer thereby reflecting the signature of the basal food source (Deniro and Epstein, 1978; Peterson and Fry, 1987; Post, 2002). Recent studies consider the variance of stable isotope signatures as a measure of the dietary niche width of consumers (Bearhop et al., 2004), a concept that has been expanded to the isotopic niche as a measure of niche dimensions of Hutchinson's (1957) *n*-dimensional hyper volume of an organisms ecological niche (Newsome et al., 2007).

A number of studies successfully used natural variations in stable isotope ratios to evaluate the trophic structure of soil animal communities (Ponsard and Arditi, 2000; Scheu and Falca, 2000; Halaj et al., 2005; Okuzaki et al., 2009; Pollierer et al., 2009), however, they either ignored Mesostigmata or included only few species. Using stable isotope methodology the present study for the first time investigates the trophic ecology of a wide range of Mesostigmata species. Forty species from 14 families of temperate deciduous forests were analyzed covering a wide spectrum of morphologies and behaviors of Mesostigmata. Assuming that the relative position in dual isotope space reflects the trophic niche of species we expected to be able to identify guilds with different prey spectra. By evaluating their trophic position under natural conditions in the field and by including basal resources of the soil animal food web the study aims at contributing to the understanding of this important predator group and their feeding interactions in soil food webs.

Furthermore, the study analyzes the relationship between body mass and trophic position in Mesostigmata. Body size is a major structuring factor of the architecture of food webs (Brose, 2010), especially predator–prey interactions strongly depend on body mass ratios (Vucic-Pestic et al., 2010; Kalinkat et al., 2011) and trophic level has been shown to increase with body size (Woodward and Hildrew, 2002; Riede et al., 2011). Therefore we expected that (1) large species occupy higher trophic levels than small species. Further, we hypothesized that (2) actively hunting Veigaiidae and Parasitidae occupy the highest trophic level due to intra-guild predation. In addition, we expected (3) nematode feeders, such as Uropodina and Zerconidae, to occupy low trophic levels by relying predominantly on decomposer prey species. Furthermore, we hypothesized that (4) isotope signatures of Mesostigmata change during ontogenesis, reflecting a change in prey spectrum with increase in body size.

2. Materials and methods

2.1. Sampling and extraction of soil animals

Eight old growth beech stands were sampled in spring 2008. The study sites were located in the Hainich-Dün region, which is situated in a low mountain range in Central Germany and features large unfragmented forests composed primarily of beech (*Fagus sylvatica*). The Hainich-Dün is among the largest regions in Central Europe covered by beech forests spanning over about 1300 km^2. The study sites form part of the "Biodiversity Exploratories", a large integrative biodiversity project (Fischer et al., 2010). Four of the selected sites have been left unmanaged since approximately 60 years, four sites were age class stands with a mean tree age of approximately 80 years; all sites were dominated by mature beech trees. The understory consisted of beech seedlings and spring geophytes, such as *Allium ursinum*, *Anemone nemorosa* and *Galium odoratum*. Parent material at the sites was loess over triassic limestone, soils were characterized as luvisols with mull or mull-like moder humus. Two small soil cores (5 cm Ø) were taken at each site for an inventory of species of Mesostigmata. For stable isotope measurements larger soil cores (20 cm Ø) were taken, two in age class stands and four in unmanaged stands. The litter layer and the upper 5 cm of each soil core were extracted separately using a modified heat extractor (Macfadyen, 1961; Kempson et al., 1963).

2.2. Identification of species and preparation of samples

Mesostigmata species were identified using Karg (1989a, 1993). Animals were transferred into tin capsules and dried at 60 °C for 24 h before measurement of stable isotopes. Three replicates per species from different sites were prepared if possible. For small and less common species individuals had to be pooled across sites; up to 70 individuals were pooled to gain the amount of material necessary for stable isotope analysis. For the species *Dinychus perforatus*, *Trachytes aegrota*, *Trachytes pauperior*, *Uropoda cassidea* and *Uroseius cylindricus* (for authorities see Appendix 1) three to four samples of adult females, deutonymphs and protonymphs (*U. cassidea* and *U. cylindricus* only) were prepared to analyze variations in stable isotope signatures with life stage. For *D. perforatus* and *U. cassidea* samples of adult males were included to inspect potential differences between sexes. In total, 146 samples of 40 Mesostigmata species (see Appendix 1) were analyzed. Soil and litter material was dried, ground with a ball mill (Retsch Mixer Mill MM200, Haan, Germany) and transferred into tin capsules for measurement of stable isotopes. Additionally, stable isotope signatures of representative macrofauna predators (Chilopoda) and decomposers (Diplopoda) were measured and included for comparison (see Appendix 2).

2.3. Stable isotope analysis

Stable isotope ratios were determined using a coupled system of an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany) (Reineking et al., 1993). Isotope signatures are expressed using the δ notation with $\delta X\ (‰) = (R_{sample} - R_{standard})/R_{standard} \times 1000$, where X represents the target isotope and R the ratio of heavy to light isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively). Nitrogen in atmospheric air served as standard for $\delta^{15}N$ and Vienna PD Belemnite as standard for $\delta^{13}C$ measurements. All animal stable isotope signatures were calibrated to the mean of the leaf litter signature of the respective sampling site to account for local variability in stable isotope signatures of basal resources.

2.4. Data analysis

Statistical analyses were performed using R 2.13.1 (R Development Core Team, 2008) and the R Commander GUI (package "rcmdr"; Fox, 2005). All data were tested for heteroscedasticity within grouping variables using Levene's test (function "leveneTest") and log transformed to improve homogeneity of variances if necessary. Single factor analysis of variance (function "aov") or a general linear model (function "lm") in case of unequal number of samples per group (ontogenetic stage or sex) was used to test for significant differences between $\delta^{13}C$ and $\delta^{15}N$ signatures of different sexes and between juvenile stages and adults (of both sexes if possible) of the species studied.

Linear regression (function "lm") using the dry weights of adult individuals and their respective $\delta^{15}N$ signature was used to inspect if the trophic level of species increases with body mass. Linear regression using the relative abundances of species and their respective $\delta^{13}C$ signatures was used to inspect if isotope signatures vary with the density of species. Linear regression using the relative abundance of species and their $\delta^{15}N$ signatures was used to inspect if the abundance of species is related to trophic level.

Convex hull envelopes were generated for the bivariate ($\delta^{13}C$ and $\delta^{15}N$) isotope signatures and total areas of the respective hulls determined using the function "laymanmetrics" of the package "SIAR" in R (Parnell et al., 2011). Threshold values for species with 5%, 2% and 1% relative abundance were used to compare the isotopic niche width of species differing in density. Additionally, convex hull envelopes were generated for species of genera with at least three samples of two or more species measured for a visual comparison of isotopic niches of related species.

3. Results

3.1. Basal resources

Leaf litter stable isotope signatures differed little between the study sites, spanning 1.08 δ units in ^{13}C (−29.43‰ to −28.35‰) and 2.15 δ units in ^{15}N (−5.39‰ to −3.24‰). Soil stable isotope signatures were more variable, spanning 4.17 δ units in ^{13}C (−30.11‰ to −25.94‰) and 3.81 δ units in ^{15}N (−1.95‰ to 1.89‰).

3.2. Adult Mesostigmata

Stable isotope signatures of adult Mesostigmata were enriched by at least 3.44‰ in ^{13}C and 1.01‰ in ^{15}N relative to leaf litter and varied considerably between species. $\delta^{13}C$ signatures of the species studied spanned 3.64 δ units ranging from *Rhodacarellus kreuzi* with −24.91‰ to *U. cylindricus* with −21.27‰ (Fig. 1). Respective $\delta^{15}N$ signatures spanned 8.77 δ units ranging from *Leitneria granulata* with −2.23‰ to *Zerconopsis remiger* with 6.54‰ (Fig. 1). $\delta^{15}N$ signatures also varied within species e.g., in *Pachylaelaps longisetus* they spanned 4.08 $\delta^{15}N$ units (Fig. 1).

3.3. Variations with ontogenetic stage, sex and body size

In *U. cylindricus* and *U. cassidea* $\delta^{13}C$ and $\delta^{15}N$ signatures of protonymphs, deutonymphs and adults were measured. They did not differ significantly in *U. cylindricus* ($F_{2;6} = 1.12$, $p = 0.39$ and $F_{1;4} = 2.32$, $p = 0.35$, respectively) but in *U. cassidea* this only applied to $\delta^{13}C$ signatures ($F_{2;11} = 0.05$, $p = 0.96$) whereas $\delta^{15}N$ signatures differed significantly between protonymphs and adults ($F_{2;11} = 6.74$,

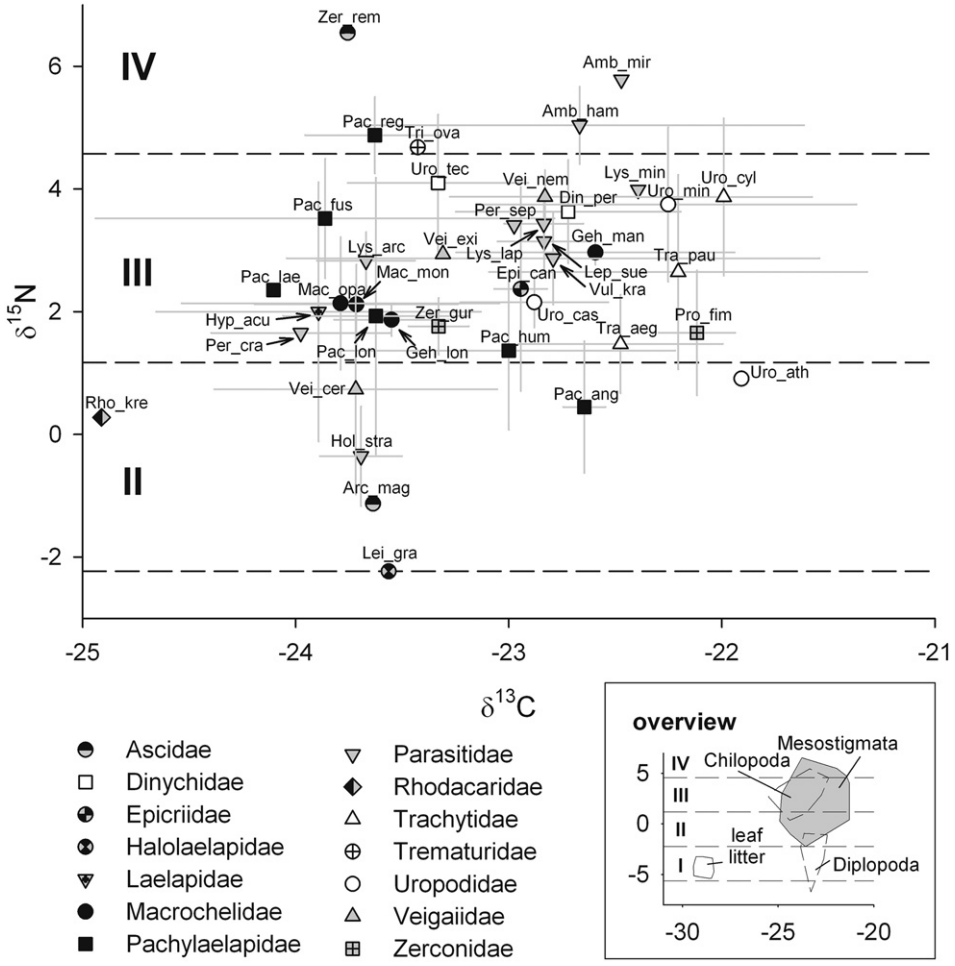

Fig. 1. Mean (±SD) stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of Mesostigmata species in old-growth beech stands; polygons in the inlet represent convex hulls enveloping bivariate ($\delta^{13}C$ and $\delta^{15}N$) isotope signatures of Mesostigmata, Chilopoda, Diplopoda and leaf litter for comparison. Dashed horizontal lines represent estimated trophic level boundaries with each trophic level spanning 3.4‰, based on the mean $\delta^{15}N$ signature of leaf litter, a mean trophic level enrichment of 0.5‰ for primary decomposers (Vanderklift and Ponsard, 2003) and 3.4‰ for higher consumer levels (Minagawa and Wada, 1984; Post, 2002); I = primary decomposers, II = secondary decomposers and first order predators, III = second order predators, IV = third order predators; different symbols indicate different families of Mesostigmata; for full species names see Appendix 1.

$p = 0.0123$), decreasing from protonymphs (2.66 ± 0.40‰) to deutonymphs (2.25 ± 0.02‰) to adults (2.03 ± 0.24‰).

Neither $\delta^{13}C$ nor $\delta^{15}N$ signatures differed significantly in any of the species in which we measured deutonymphs and adults ($F_{1;8} = 0.01$, $p = 0.92$ and $F_{1;8} = 1.40$, $p = 0.26$ for *Dinychus perforatus*, respectively; $F_{1;9} = 2.03$, $p = 0.19$ and $F_{1;9} = 1.57$, $p = 0.24$ for *T. aegrota*, respectively; $F_{1;4} = 0.01$, $p = 0.97$ and $F_{1;4} = 0.06$, $p = 0.81$ for *T. pauperior*, respectively).

Similarly, neither $\delta^{13}C$ nor $\delta^{15}N$ signatures differed significantly between adult males and females in the two species analyzed ($F_{1;4} = 0.68$, $p = 0.46$ and $F_{1;4} = 0.13$, $p = 0.74$ for *D. perforatus*, respectively; $F_{1;6} = 0.31$, $p = 0.60$ and $F_{1;6} = 0.11$, $p = 0.75$ for *U. cassidea*, respectively).

Linear regression indicated that $\delta^{15}N$ signatures neither significantly increased with body mass in the dataset of all adults ($r^2 = 0.01$, $p = 0.35$, Fig. 3), nor in subsets of data including only Parasitidae and Veigaiidae ($r^2 = 0.03$, $p = 0.35$), or Uropodina and Zerconidae ($r^2 = 0.04$, $p = 0.18$).

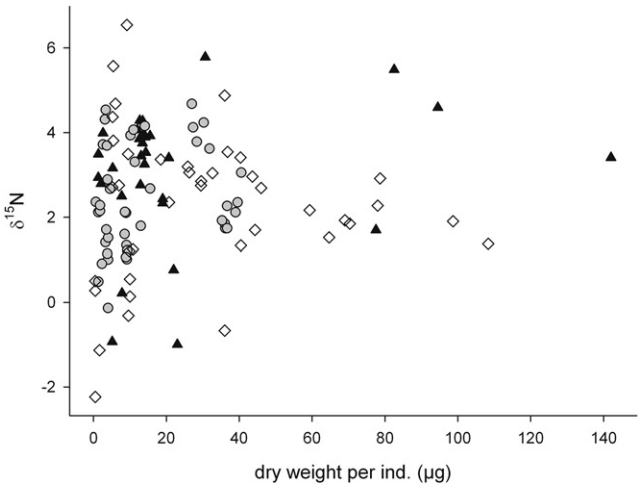

Fig. 3. Relationship between body size and trophic level as indicated by $\delta^{15}N$ signatures of adult Mesostigmata; none of the regression calculated for all species, arthropod hunting Parasitidae and Veigaiidae (black triangles), and nematode feeding Uropodina and Zerconidae (open diamonds) were significant ($p > 0.05$).

3.4. Variations in isotopic niches

The area covered by the bivariate isotope signatures (total area) of Mesostigmata increased gradually when including less common species (Fig. 2a). Total area increased from 9.74 for the threshold of 5% relative abundance of the species included, to 14.02 for the 2%, 21.77 for the 1% threshold and 22.99 for all species studied. Linear regression indicated increasing $\delta^{13}C$ signatures with increasing relative abundance of species ($r^2 = 0.13$, $p = 0.0001$; Fig. 2b), but no such increase in $\delta^{15}N$ signatures ($r^2 = 0.01$, $p = 0.92$).

While signatures of species of different families frequently overlapped (Fig. 1), signatures of closely related species (i.e., species of the same genus) often formed distinctly separated planes in dual isotopic space. In the genera *Uropoda* (Fig. 4a), *Pachylaelaps* (Fig. 4b) and *Geholaspis* (Fig. 4d) the hull areas of the species studied were fully separated. In the genus *Veigaia* hull areas of *Veigaia cerva* and *Veigaia nemorensis* were also distinct, but the dot of the singular measurement of *Veigaia exigua* was located at the border of the hull area of *V. nemorensis* (Fig. 4c). The hull area of *T. aegrota* in part overlapped with that of *T. pauperior* (Fig. 4e), due to very variable $\delta^{15}N$ signatures in *T. pauperior*, which spanned 4.13 δ units. The genus *Macrocheles* was exceptional with similar $\delta^{13}C$ and $\delta^{15}N$ signatures of *Macrocheles montanus* and *Macrocheles opacus aciculatus* (Fig. 4f).

4. Discussion

All 40 analyzed Mesostigmata species were strongly enriched in $\delta^{15}N$ relative to leaf litter with signatures similar to those of large arthropod predators, such as spiders, staphylinids and centipedes (Scheu and Falca, 2000; Pollierer et al., 2009). This indicates that irrespective of their small body size, Mesostigmata occupy high trophic positions in the soil food web. The broad range of $\delta^{13}C$ and $\delta^{15}N$ signatures supports the view that Mesostigmata species feed on a variety of prey from different trophic levels and feeding types. Prey taxa, such as Collembola, Nematoda and other Acari (Karg, 1989a, 1993; Koehler, 1999; Heidemann et al., 2011), comprise primary and secondary decomposers as well as predators (Schneider et al., 2004; Chahartaghi et al., 2005; Maraun et al., 2011). Assuming a ^{15}N enrichment of 3–4‰ per trophic level (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Post, 2002) the span of $\delta^{15}N$ of 8.4‰ suggests that Mesostigmata utilize prey from all three trophic levels.

All Mesostigmata species studied were also enriched in ^{13}C compared to leaf litter, indicating that their prey relies on carbon sources with a more enriched $\delta^{13}C$ signature than bulk leaf litter

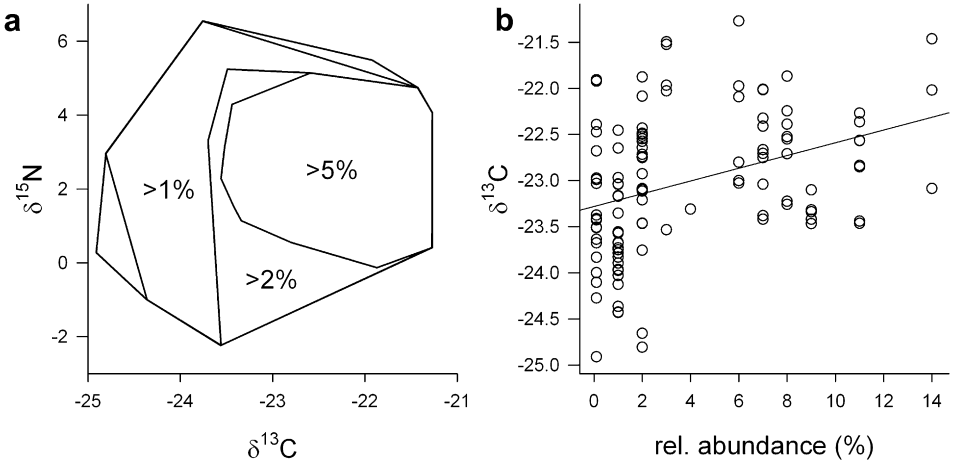

Fig. 2. (a) Total area occupied by Mesostigmata in dual ($\delta^{13}C$ and $\delta^{15}N$) isotopic space as related to the relative abundance of species; the outermost line represents the convex hull envelope of all species analyzed, successively smaller areas represent convex hulls for thresholds of relative abundances equal to 1%, 2% and 5%; (b) relationship between relative abundance and $\delta^{13}C$ signatures in Mesostigmata (linear regression, $r^2 = 0.13$, $p < 0.001$).

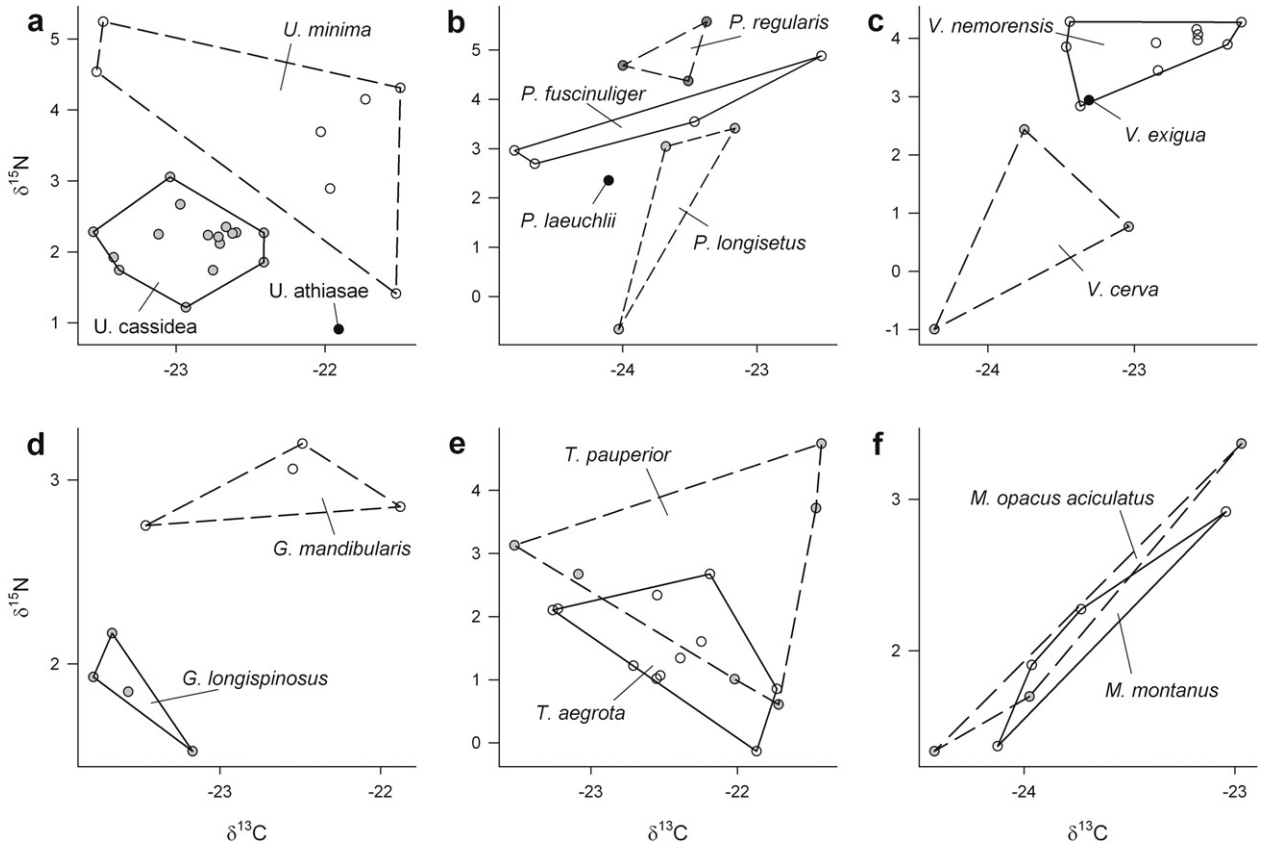

Fig. 4. Isotopic niches of species of the same genus co-occurring in old-growth beech stands; polygons represent convex hulls enveloping the bivariate ($\delta^{13}C$ and $\delta^{15}N$) isotope signatures of each species; filled circles represent single measurements; for full species names see Appendix 1.

material. A similar enrichment was found throughout studies on natural isotope ratios of carbon in forest soil animals (Ponsard and Arditi, 2000; Okuzaki et al., 2009; Pollierer et al., 2009; Semenyuk and Tiunov, 2011). This increase in $\delta^{13}C$ values suggests that soil animal food webs rely in large on plant components less depleted in ^{13}C than bulk plant litter (Pollierer et al., 2009). As suggested previously, the use of root-derived resources may significantly contribute to the shift in $\delta^{13}C$ values between plant tissue and soil animal species (Pollierer et al., 2007) as phloem sap $\delta^{13}C$ signatures of beech (forming the basis of root exudates) are high (Gessler et al., 2004). High $\delta^{13}C$ signatures of basal species are passed on to predators which rely almost exclusively on prey from the decomposer subsystem (Scheu, 2001, 2002; Miyashita et al., 2003; Oelbermann et al., 2008).

Compared to the large range of isotopic signatures of all Mesostigmata species studied, the dominant species occupied a relatively narrow range of $\delta^{13}C$ and $\delta^{15}N$ signatures, indicating that most of their prey species occupy similar and rather narrow niches. $\delta^{15}N$ signatures of the dominant Mesostigmata species were in the range of second order predators suggesting that secondary decomposers (and potentially also first order predators) form the dominant prey of Mesostigmata, whereas primary decomposers are of minor importance. It is increasingly recognized that primary decomposers form only a small fraction of soil animal species among e.g., Diplopoda (Pollierer et al., 2009; Semenyuk and Tiunov, 2011), Lumbricidae (Schmidt et al., 2004; Pollierer et al., 2009), Collembola (Chahartaghi et al., 2005) and Oribatida (Schneider et al., 2004; Maraun et al., 2011). Typically, these groups are well protected against predation due to large body size, strong sclerotization and/or chemical defense and therefore contribute little to predator nutrition (Scheu, 2002).

$\delta^{13}C$ signatures of most of the dominant Mesostigmata species were high. This may be due to high contribution of prey from deeper soil strata, since $\delta^{13}C$ signatures increase with soil depth (Bostrom et al., 2007) and soil dwelling species therefore are more enriched in ^{13}C (Tiunov, 2007). However, species included in this study predominantly colonize the litter and uppermost soil layer; prey species therefore likely also originated predominantly from these layers and not from deeper soil layers. Most of the species of the hull area of dominant species are slow moving and possess small pincer-like chelicerae (e.g., Uropodina and Zerconidae). Commonly, this is considered to indicate nematode feeding (Buryn and Brandl, 1992; Koehler, 1999). However, the hull area also comprised species with larger chelicerae and a more active foraging behavior such as *Pergamasus septentrionalis* and *V. nemorensis*. *P. septentrionalis* recently has been shown to also feed on nematodes in the field using molecular gut content analysis (Peschel et al., 2006; Heidemann et al., 2011) and *V. nemorensis* readily consumes nematodes in the laboratory (B. Klarner, pers. observation). This suggests that the diet of dominant Mesostigmata species consists in large of nematode prey; unfortunately, due to the small body size, stable isotope data of nematodes of temperate forests are not available. Nematodes at our study sites comprise mainly bacterial feeders (~50%), plant (root) feeders (~35%), fungal feeders (<5%) and predators (<5%; L. Ruess, pers. comm.). This suggests that among nematodes of old growth beech forests bacterial and root feeding species form the main prey of Mesostigmata. This supports the view that bacteria form an important component of the diet of higher order consumers and bacterial carbon is channeled to top level predators of soil food webs (Crotty et al., 2011; Pollierer et al., 2012).

Low $\delta^{13}C$ signatures, i.e., signatures closer to those of plant litter, mainly occurred in Collembola hunting specialists such as *Pergamasus crassipes* and *V. cerva*, in generalists such as *Hypoaspis aculeifer*, but also in Macrochelidae and Pachylaelapidae, which are assumed to mainly feed on – compared to nematodes – large "worm like" prey such as Diptera larvae and Enchytraeidae (Koehler, 1999). These Mesostigmata species likely occupy trophic niches similar to those of macrofauna predators such as Chilopoda. Their $\delta^{15}N$ signatures also indicate feeding on secondary decomposers. Overall, stable isotope signatures and literature data suggest that their prey predominantly comprises fungal feeding Collembola rather than Nematoda. This is consistent with the low $\delta^{13}C$ signatures of these Mesostigmata species resembling signatures of saprotrophic litter decaying fungi (Bostrom et al., 2008). Low relative abundances in this group further support the view that complex litter compounds are utilized predominantly by microbial decomposers with little of this carbon passed on to higher consumer levels (Pollierer et al., 2007).

Some species, such as *Z. remiger*, *Pachylaelaps regularis* and both *Amblygamasus* species, had exceptionally high $\delta^{15}N$ signatures pointing to intra-guild predation (Ponsard and Arditi, 2000; Halaj et al., 2005). *Amblygamasus hamatus* and *Amblygamasus mirabilis* are comparatively large and therefore may feed on other Mesostigmata; *Z. remiger* and *P. regularis* are rather small and therefore likely feed on predatory Nematoda and/or small predatory/scavenging Collembola.

Body size also varied considerably in species of the lower and medium range of $\delta^{15}N$ signatures. Predator size typically increases with trophic level (Riede et al., 2011), but this appears not to be the case in Mesostigmata as their $\delta^{15}N$ signatures were not related to body mass. Body size of species of nematode feeders, such as Uropodina and Zerconidae, and active arthropod hunters, such as Parasitidae and Veigaiidae, also spanned over a wide range suggesting that prey of both of these predator guilds originates from a broad range of trophic levels and size classes.

Generally, stable isotope signatures varied little with developmental stage and sex suggesting that the prey spectrum of the studied species is rather constant irrespective of body size and sex. However, the slightly decreasing $\delta^{15}N$ signatures with successive developmental stage in *U. cassidea* indicate that in this species the prey spectrum changes during ontogeny, but the changes are moderate. In some species (e.g., *P. longisetus*) stable isotope signatures of adults varied markedly suggesting generalistic feeding on locally abundant prey.

Signatures of species of different taxonomic affiliation (different family) overlapped widely. In part this is due to the fact that signatures of species of certain families e.g., Parasitidae, spread across large ranges in bivariate isotopic space. Therefore, characters used to define higher taxonomic units such as families are not related to the feeding mode or food spectrum. On the contrary, trophic niches of closely related Mesostigmata species i.e., species from the same genus, such as *P. regularis*, *Pachylaelaps fuscinuliger*, *Pachylaelaps laeuchlii* and *P. longisetus*, often were separated markedly in at least one of the two isotopic niche dimensions. This indicates that trophic niche partitioning contributes to the coexistence of morphologically similar species and may have contributed to diversification of Mesostigmata species. However, in some cases related species apparently occupy similar niches e.g., isotope signatures of *M. montanus* and *M. opacus aciculatus* were similar. Species of this genus are assumed to feed on Diptera larvae and Nematoda developing in temporarily available resources such as decaying plant remains or dung (Koehler, 1999). Predators in food webs of such resource patches with a single basal resource are likely to have similar stable isotope signatures, and communities in such habitats are unlikely to be structured by competition for resources thereby allowing coexistence of trophically similar species.

The amount of material needed for stable isotope analysis currently necessitates to pool samples of small animals for measurement. This limits the analysis of variations in the isotope signatures of small soil animal species. Lowering detection thresholds for ^{13}C and ^{15}N in mass spectrometry is needed to allow deeper insight into the role of niche partitioning in meso- and micro-fauna soil food webs. More individual based data of soil animals will allow evaluating community wide isotopic niche width metrics, an approach that has been successfully used in aquatic food webs (Layman et al., 2007; Jackson et al., 2011).

5. Conclusions

Overall, stable isotope signatures reflect that the prey of mesostigmatid mites is diverse with individual species occupying distinct niches which vary little with ontogenetic stage and sex. Notably, related species usually have well separated trophic niches. $\delta^{15}N$ signatures suggest that most of the prey of Mesostigmata comprises secondary decomposers with primary decomposers and intra-guild prey being less important. Presumably, due to the varying body size of their prey the trophic position of Mesostigmata does not increase with body size. Dominant species likely feed to a large extent on nematodes with their prey relying strongly on root derived carbon. Less abundant species presumably rely more on fungal feeding species such as Collembola obtaining their carbon from saprotrophic fungi i.e., from the plant litter energy channel. More detailed studies employing fatty acid and molecular gut content analysis are needed to fully appreciate the complex feeding relationships in soil food webs and the role of Mesostigmata therein.

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Appendix A. Supplementary data

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.soilbio.2012.08.013.

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