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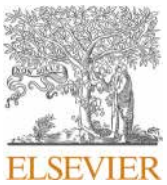

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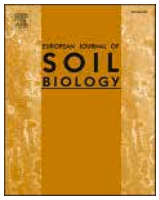

Original article

Trophic niche variation in springtails across soil depth

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ABSTRACT

Soil invertebrates move vertically through the soil to forage and avoid environmental stress. However, how their diet shifts with depth remains poorly understood, limiting our understanding of their trophic plasticity. Trophic consistency across depths could result from similar trophic niches existing at the microscale within different soil layers (the micro-scale feeding hypothesis). To test this, we conducted a microcosm experiment incubating springtails (*Ceratophysella denticulata*) in six separate forest soil layers (O_L, and $O_{F/H}$, and 0–3, 3–6, 6–9 and 9–12 cm depth of the mineral soil) and analysed changes in Collembola stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$). As expected, $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in litter and soil organic matter increased with depth, whereas $^{13}C/^{12}C$ ratios of Collembola did not significantly differ across layers suggesting consistent basal resource use supporting the micro-scale feeding hypothesis. By contrast, $^{15}N/^{14}N$ ratios of Collembola increased with depth, following the trend of organic matter from O_L to 0–3 cm soil, but not beyond. These results suggest that carbon and nitrogen nutrition of springtails is decoupled, and that the use of litter to calibrate $^{15}N/^{14}N$ values for estimating trophic positions of soil animals requires careful interpretation. Our results highlight the importance of soil depth as determinant of trophic positions of soil animals and point to principle differences in nitrogen resource acquisition between litter and soil in soil animal decomposers. Overall, the vertical structure of soils and a microscale view of trophic interactions needs closer attention to better understand niche differentiation and resource acquisition of soil animals.

1. Introduction

Soil is heterogeneous [1,2] and a key element of this heterogeneity is soil depth, which is associated with changes in the availability of food resources and habitable pore space for soil organisms. Soil microarthropod species are adapted to live at different depths in soil, but mostly live in the organic layer and the upper mineral soil. To forage for food or avoid abiotic stress such as desiccation, microarthropods and other soil animals move between soil layers [3–5]. Moving to different layers may be associated with changes in feeding habits, but studies analysing trophic niches of animal species sampled at different depths showed little change [6,7]. Field studies, however, cannot disentangle whether this consistency is (i) due to soil animals predominantly feeding only at a specific depth despite moving between layers, or (ii) due to feeding on microsites with similar stable isotope signatures across soil depths [6,7]. Therefore, to what extent soil depth affects the trophic niche of soil animals remains poorly understood. This gap of knowledge hampers our understanding of the trophic niche of soil animal species and their trophic plasticity and thereby the diversity of soil animal species [6,8,9].

Over the last twenty years, bulk C and N stable isotope analyses have allowed to analyze and understand the trophic structure of soil animal communities in unprecedented detail and accuracy [6,10,11]. It is well established that microarthropod groups include species of different trophic positions, ranging from primary to secondary decomposers and predators [12–14]. However, one of the uncertainties in using bulk stable isotope ratios to estimate trophic niches of soil animals is the use of litter as isotopic baseline regardless of the vertical localization of soil animals along soil depth [11]. Although many deep soil living animals such as euedaphic Collembola and endogeic earthworms are relatively

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enriched in ^{13}C and ^{15}N [15], the reason for this shift is not well understood. One potential explanation is that using litter as baseline may not reflect the true trophic position of soil animals if they feed on resources from deeper soil typically being enriched in ^{15}N [7,11,16]. Despite this enrichment, existing studies suggest that trophic niches of the same species are highly consistent irrespective of the depth they inhabit [6,7]. Potentially, soil animals feed in microsites on resources of similar stable isotope signature, regardless of the enrichment in bulk ^{15}N and ^{13}C with depth (hereafter named micro-scale feeding hypothesis) [7,17,18].

Here, we aimed at testing whether the variation in trophic niches of soil microarthropods across soil depth can be explained by the vertical movement of animals or by selective feeding on microsites with similar isotopic signature. The content of ^{15}N allows tracing the trophic level of consumers and the content of ^{13}C allows tracing the use of basal resources in food webs [11,19]. We tested two alternative hypotheses: (1) Collembola stable isotope values follow those of the organic matter in the respective litter/soil layer they were incubated, i.e. Collembola adjust their nutrition to the local resources available reflecting trophic plasticity (Fig. 1a), (2) stable isotope values of Collembola do not change with soil depth, i.e. do not follow the changes in stable isotope values of the organic resources with soil depth reflecting trophic consistency and supporting the micro-scale feeding hypothesis (Fig. 1b). The results are also expected to provide insight into potential biases in the estimation of trophic positions due to using litter as baseline.

2. Methods

2.1. Field sampling

Soil cores (ø 5 cm, >15 cm height) were taken in a mature European beech (*Fagus sylvatica* L.) forest near Dassel in the Solling mountain, Germany (51.723°N, 9.708°E) on October 18, 2022. Five replicate soil cores were taken >5 m apart. Each soil core was carefully sliced into litter (O_L), fragmentation/humus layer ($O_{F/H}$) and four soil depths of 3 cm thickness of the A_h layer (0–3, 3–6, 6–9, 9–12 cm depth; Fig. 1a). The samples were kept intact, stored at −20 °C for two weeks and then freeze-dried for defaunation [20]. Then, distilled water was added to reestablish field moisture content (Table S1) and 1-6-day old juveniles of Collembola were added [21]. The forest soil used developed from Triassic sandstone and is classified as Dystric Cambisol (FAO-ERB 2014) [22]. The O_L and $O_{F/H}$ layer contained 42 % and 23 % organic carbon (Table S1). The soil texture was silt loam (clay 21 %, silt 53 %, sand 26 %).

2.2. Collembola synchronisation

We used *Ceratophysella denticulata* (Collembola) for this experiment because this species occurred at our study sites and lives in organic and mineral soil layers across temperate forests [23,24]. Cultures of *C. denticulata* were synchronized in Petri-dishes with a bottom layer of plaster of Paris/charcoal mixture. Plaster of Paris was saturated with water before adding twenty adults of *C. denticulata*. Directly after their addition, Collembola were fed with moist baker's yeast and incubated for three days at 20 °C. At the end of incubation, adults and yeast were removed. Collembola juveniles started to hatch eleven days after removal of adults and were added into microcosm within three days using a pooter.

2.3. Experimental design

To each of the six layers we added five individuals of 1–6 days old juvenile *C. denticulata* and incubated them in closed jars to keep moisture constant in the dark at 20 °C for 4 weeks (Fig. 1). Each of the six soil layers was replicated five times resulting in a total of 30 microcosms. Once per week, jars were opened for about 20 min for aeration. At the end of the experiment, Collembola were extracted by heat for 7 days [25] and isotope ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were measured in bulk

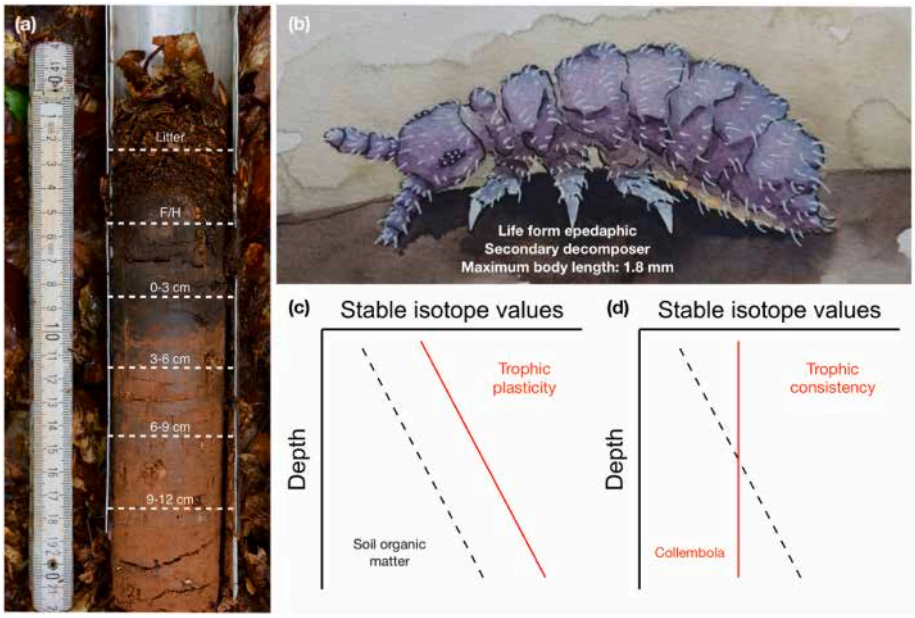

Fig. 1. (a) Image of the soil depth gradient and (b) soil Collembola species (*Ceratophysella denticulata*) studied, as well as (c, d) graphical representation of the two alternative hypotheses investigated on changes in the trophic niche (stable isotope value) of decomposer animals with soil depth. The soil layers included Litter (O_L), Fragmentation/Humus layer ($O_{F/H}$), and four 3 cm soil layers (0–12 cm depth) obtained from a single soil core; a total of five soil cores were investigated (5 replicates). Litter and soil were defaunated, inoculated with *C. denticulata* and incubated separately. The hypotheses tested include (c) decomposer animals feed on resources based on bulk soil organic matter in the respective layer reflecting trophic plasticity, and (d) decomposer animals feed on the same food resources across soil layers thereby occupying a consistent trophic niche regardless of changes in stable isotope values of bulk litter and soil organic matter with soil depth (micro-scale feeding hypothesis). The black dashed line represents stable isotope values in bulk litter and soils, and the red solid line those of decomposer animals. Watercolour painting of Collembola provided by Svenja Meyer.

soil material and in bulk animal tissue [7].

2.4. Bulk stable isotope analysis

Bulk stable isotopes of litter and soil were measured after drying at 60 °C and grinding samples in a ball mill (MM200, Retsch, Haan, Germany). Collembola were extracted into 50 % diethylene glycol within a week and then transferred into 70 % ethanol for storage. Storage in ethanol little affects the isotope composition of animals [26,27] and, since all animals were treated in the same way, storage in ethanol unlikely affected our results. As Collembola dry weight typically was <100 µg, bulk stable isotope ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were measured using a modified setup adopted for small sample size [28]. Atmospheric nitrogen and Vienna PeeDee belemnite were used as primary standards. On average two individuals were lumped for stable isotope analysis for each microcosm (mean and SD tissue dry biomass of 12.4 ± 0.8 µg). Acetanilide (C_8H_9NO, Merck, Darmstadt, Germany) was used as internal standard. Natural variation in stable isotope ratios of carbon and nitrogen (X) were expressed as δX (‰) = $(R_{sample} - R_{standard})/(R_{standard}) \times 1000$, with R the ratio between the heavy and light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$). Bulk isotope values of the respective layer were used to calibrate isotope values of Collembola (denoted as $\Delta^{13}C$ or $\Delta^{15}N$); non-calibrated isotope values are denoted as $\delta^{13}C$ or $\delta^{15}N$ (Fig. 2).

2.5. Data analysis

Linear mixed-effects models (LMMs) were used to analyze variations in $\delta^{13}C$ and $\delta^{15}N$ values in bulk material, and non-calibrated $\delta^{13}C$ and $\delta^{15}N$ values of Collembola and calibrated $\Delta^{13}C$ and $\Delta^{15}N$ values of Collembola to the respective bulk material (litter/soil). Soil depth was treated as fixed effect including six levels and the five replicate cores were treated as random effect, with each core being considered as a block. The heterogeneity of residuals was resolved by allowing residual variance to differ between depths [29]. Differences between means were inspected using the contrast function in the 'emmeans' package with litter as reference. One bulk ^{13}C data point was beyond three times standard deviation around the mean and was considered as outlier not included in the analysis. We checked that excluding the outlier did not change main statistical outcomes (depth effects with outlier $F_{5,17} = 0.53$, $P = 0.74$ and without outlier $F_{5,16} = 0.56$, $P = 0.73$). All analyses were done in R v4.0.3 (https://www.r-project.org/). We used the 'nlme' package to fit LMMs (Bates et al., 2015) and the 'emmeans' to estimate marginal means. All final LMMs met the assumptions of normality of residuals and homogeneity of variance.

3. Results

Stable isotope values of juvenile Collembola used in the experiment were −22.2 ± 0.5 ‰ and 2.9 ± 0.5 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Individual biomass of Collembola changed from initially about 1 µg to on average of 7.6 µg at the end of the experiment. Bulk litter and soil materials were consistently enriched in ^{13}C and ^{15}N with soil depth (Table S2, Fig. 2a–d), whereas $\delta^{13}C$ values of Collembola did not vary significantly with soil depth (Fig. 2b). Collembola $\delta^{15}N$ values were significantly enriched compared to bulk litter/soil in the respective litter/soil layer up to 0–3 cm soil depth, but not further (Fig. 2f). Furthermore, $\delta^{15}N$ values of Collembola were similar across soil layers except in the O_L layer ($F_{4,12} = 1.5$, $P = 0.25$ for the effect of depth with the O_L layer excluded; Fig. 2e).

4. Discussion

As soil layers were incubated separately and Collembola were only able to feed on the respective litter/soil layer they were incubated in, the observed consistency in $\delta^{13}C$ values of Collembola suggests that they fed on microsites colonized by microorganisms using organic matter resources of similar stable isotope $\delta^{13}C$ signatures across litter/soil layers, supporting the micro-scale feeding hypothesis. By contrast, $\delta^{15}N$

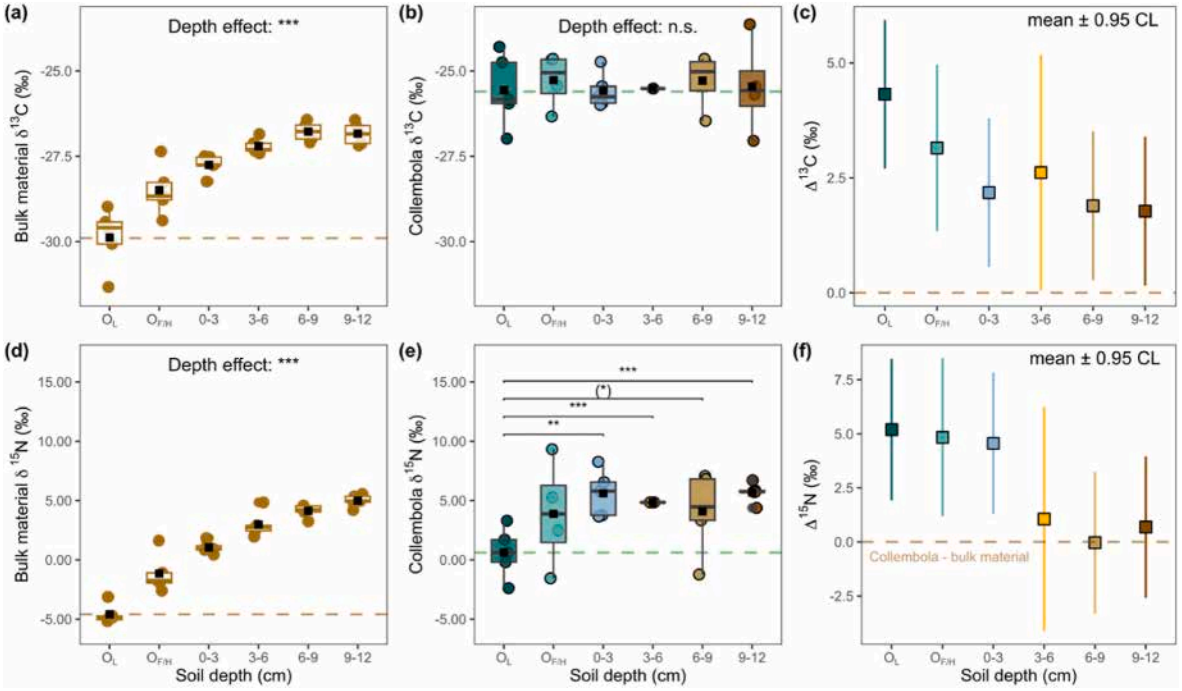

Fig. 2. Variations in stable isotope ratios in bulk organic matter and *Ceratophysella denticulata* with soil depth [litter layer (O_L), fragmentation/humus layer ($O_{F/H}$) and four mineral soil depths (0–3, 3–6, 6–9, 9–12 cm)]. (a) $\delta^{13}C$ values in bulk organic matter, (b) $\delta^{13}C$ values in *C. denticulata*, and (c) differences in $\delta^{13}C$ values between *C. denticulata* and bulk organic matter ($\Delta^{13}C$); (d) $\delta^{15}N$ values in bulk organic matter, (e) $\delta^{15}N$ values in *C. denticulata*, and (f) the difference in $\delta^{15}N$ values between *C. denticulata* and bulk organic matter ($\Delta^{15}N$). Square dots represent arithmetic means; CL, confidence level; asterisks indicate the level of significance, (*) $p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

signatures of Collembola increased with depth, following the trend of organic matter from litter to 0–3 cm soil, but not beyond, suggesting that carbon and nitrogen nutrition of springtails is decoupled.

Typically, Collembola as well as virtually all other soil animals are enriched in ^{13}C by 3–4 ‰ compared to litter ('detrital shift'; [11,15,19]). Our study showed that the enrichment declines with soil depth when the stable isotope values of the animals are calibrated using the respective bulk stable isotope values of litter/soil in which they were incubated. However, this decrease with depth was non-linear and decreased with soil depth down to a depth of 0–3 cm of the A_H layer and then stayed constant. The increase in $\delta^{13}C$ values in soil organic matter with soil depth is likely due to the mineralization of litter compounds depleted in ^{13}C, such as lignin and waxes [30,31] and/or is related to the accumulation of microbially processed carbon. Hence, the more pronounced detrital shift in the O_L layer presumably results from undigestable plant compounds depleted in ^{13}C [15]. Presumably, the observed decline in the enrichment of ^{13}C in *C. denticulata* between the O_L layer and 0–3 cm soil depth reflects the decomposition of these compounds resulting in organic matter with more digestable compounds. This indicates that the enrichment in ^{13}C is unlikely related to changes in the resources used by detritivore soil animals such as *C. denticulata*. The fact that the enrichment in ^{13}C remained constant in deeper soil layers (0–12 cm soil depth) suggests that $\delta^{13}C$ values of soil organic matter in these layers better reflect the carbon resources used by *C. denticulata* than those in the litter layer, indicating that litter calibrated $\delta^{13}C$ values of detritivore animals need to be interpreted with caution.

Collembola $\delta^{15}N$ values were significantly enriched compared to bulk litter/soil in the respective litter/soil layer up to 0–3 cm soil depth, but not further. By contrast, $\delta^{15}N$ values of Collembola were similar across soil layers except in the O_L layer, reflecting that Collembola occupy a consistent trophic niche across soil layers, arguing in favor of the micro-scale feeding hypothesis. Consistent $\delta^{15}N$ values in Collembola except for the O_L layer further suggests that the sources of nitrogen used for tissue formation of Collembola differs between the O_L layer and the other litter/soil layers, which indicates a decoupling of carbon and nitrogen sources in the O_L layer. Due to nitrogen shortage in litter, microorganisms (and thereby also Collembola) often incorporate nitrogen from other sources such as the mineral soil or deposition [32,33] likely affecting litter $\delta^{15}N$ values [34]. Similar to ^{13}C, these findings suggest that using litter $\delta^{15}N$ values for calibrating stable isotope values of soil invertebrates should consider their depth of feeding. Using litter as baseline may only be adquate for taxa inhabiting (exclusively) the O_L layer. For taxa living in deeper soil, using the $\delta^{15}N$ values of the $O_{F/H}$ or 0–3 cm soil layer as baseline may be more adequate. However, using $\delta^{15}N$ values of organic matter of deeper soil layers (3–6 cm and below) for calibrating stable isotope values of soil invertebrates results in unrealistically low trophic positions due to the high $\delta^{15}N$ values of organic matter in deeper soil layers, which are likely due to nitrogen bound in recalcitrant compounds or associated with organo-minerals contributing little to the nutrition of decomposer soil microorganisms and invertebrates [35,36].

Soil food-web studies typically use the litter, i.e. O_L layer material, as baseline to calibrate the trophic niches of soil animals and to compare their trophic niches across ecosystems [14,37]. Our study illustrates that using litter as baseline inflates the trophic position of animals feeding below the O_L layer. Results of previous studies reporting higher trophic positions of animal species living in deeper soil layers therefore likely at least in part were due to feeding in deeper soil layers while using litter as baseline [13,38]. However, we do not advocate for abandoning the use of litter as baseline as it is useful for comparing different ecosystems, but our findings argue that care is needed in interpreting O_L layer calibrated values in a uniform way. In the field, stable isotope values of microarthropod species in litter and soil likely differ less than in our study [6,7,39] because soil animals integrate resources from different depths, either by feeding on fungal hyphae that span depths or by moving vertically. Our study prevented these mechanisms by incubating the animals in separate layers. Overall, by studying trophic niches of Collembola confined to resources in different soil depths, our results highlight the consistency of trophic niches across soil depth except in the O_L layer. The results generally support that Collembola selectively feed on similar food resources present in microsites across soil layers and underscore the importance of adopting a micro-scale view to better understand the feeding ecology of soil animals.

CRediT authorship contribution statement

Jing-Zhong Lu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Melissa Jüds:** Writing – review & editing, Validation, Resources, Project administration, Methodology. **Linlin Zhong:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Conceptualization. **Johannes Lux:** Writing – review & editing, Validation, Resources, Project administration, Methodology. **Stefan Scheu:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Amandine Erktan:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2025.103745.

Data availability

Data in "Trophic niche variation in springtails across soil depth" (Original data) (Dryad)

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