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Microhabitat more than ecosystem type determines the trophic position of springtail species

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ABSTRACT

Trophic plasticity may intensify competition among soil animal species and reduce their high diversity, which is often maintained by trophic niche differentiation and vertical microstratification in soils. Soil decomposers such as Collembola can shift their trophic niche with changing microhabitats across soil depths (vertical variation) and between different ecosystem types (horizontal variation), but these variations need further investigation. Here, we compared the stable isotope values of 27 Collembola species between litter and soil layers in 40 forest stands, comprising monocultures of European beech, Norway spruce, Douglas fir, or mixtures of European beech with either of the two conifer species. The results showed that the $\delta^{15}N$ values of Collembola within species were uniformly higher in soil than in the litter layer irrespective of forest type. This increase correlated with the biomass of Gram-negative bacteria but not with that of fungi. The $\delta^{13}C$ values of Collembola were significantly enriched in beech forests, but were similar in Douglas fir and Norway spruce forests indicating similar effects of the two coniferous species on the basal resource use of Collembola. Overall, the results suggest that Collembola shift their diet to consume local resources available in the respective soil layer they colonize, with bacteria playing a more important role in driving variations in their trophic positions than previously assumed. By contrast, the consistent trophic position of Collembola between ecosystem types suggest access to similar food sources in the soil microhabitat, despite large changes in aboveground vegetation type. Overall this study suggests that changes in ecosystem types has little influence on the resources accessible to Collembola which presumably selectively feed on specific resources in the soil microhabitat. By contrast, variations in resource types and soil microhabitats across soil depth more strongly affect the trophic niche of Collembola, which requires plasticity to adapt to their diet.

1. Introduction

When animals move to new habitats, they may feed on local resources or return to their initial habitat for food. Changing the food source, thereafter named "feeding flexibility" (Briones, 2018) increases the trophic niche width of species, especially when food resources differ between habitats. In contrast to large mammals requiring large foraging ranges, soil animals maintain high abundance and species diversity at small spatial scale (Bardgett and van der Putten, 2014). Ecologists have long been fascinated by the relationship between soil animal species diversity and the diversity of their feeding habits (Anderson, 1975; Scheu and Falca, 2000; Potapov et al., 2019b). Anderson (1975) stressed that high local biodiversity of soil invertebrates is associated with food specialization, which may be due to local excess of food, potentially undetected differences in resource utilization and/or a spatial segregation of soil animals in soil microhabitats. The use of stable isotope analysis in the past decades allowed quantifying the trophic niches of species as well as the diversity of their food resources in unprecedented

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detail (Scheu and Falca, 2000; Chahartaghi et al., 2005; Potapov et al., 2019b). However, studies investigating variations in trophic niches of soil animals between microhabitats in the field using stable isotopes are limited. This is unfortunate as this may allow answering long-standing questions in soil animal ecology such as whether species undergoing vertical migration are able to adapt to the shift in resources with soil depth.

For soil animals, microhabitats are fractions of the pore space with distinct environmental conditions or resources which can be structured horizontally or vertically at millimeter to centimeter scales (Anderson, 1975). Previous studies suggested the trophic niches of soil animals at community-level to vary between microhabitats, e.g. between dead wood and bulk soil or between moss and litter patches (Lehmitz and Maraun, 2016; Fujii et al., 2023). However, it remains unclear to what extent these shifts are due to variations in the trophic niche of species or to changes in species composition. Focusing on shifts in stable isotope composition of soil animal species with soil depth may allow to identify shifts in trophic niches of soil animal species that are relevant for virtually any soil (Potapov et al., 2019b; Erktan et al., 2020). Contrasting the perspective of high trophic plasticity of soil arthropods, the trophic niche of oribatid mites was found to be surprisingly consistent across soil layers (Scheu and Falca, 2000; Lu et al., 2022). Studies investigating variations in the trophic niche of soil animals with soil depth are limited and virtually lacking for major taxa such as Collembola (Scheu and Falca, 2000; Lu et al., 2025), despite their feeding strategy likely differs from that of oribatid mites, e.g. by foraging more on bacterial resources (Lux et al., 2024a), while oribatid mites and Collembola predominantly feed on fungi (Pollierer and Scheu, 2021). This gap hampers our understanding of how microhabitat heterogeneity affects species coexistence and trophic diversity of soil animals.

Early studies on the trophic niche of Collembola species using microscopic gut content analysis indicated that they ingest similar food resources within and across microhabitats (Ponge, 2000). However, it also has been shown that Collembola species may shift their trophic niches under environmental stress such as predatory pressure by gamasid mites or drought (Anderson, 1971; Meyer et al., 2021). Considering that Collembola species colonize different soil layers, they may ingest food resources present in the respective layers and microhabitats or cease feeding until back to their preferred soil layer and preferred food substrate. The former strategy results in broad trophic niches and high trophic plasticity, whereas the latter is associated with rather fixed trophic niches, greater trophic specialization and higher mobility. Stable isotope analysis may allow differentiating between these strategies as it provides insight into the utilization of basal resources, as indicated by the consumer $^{13}C/^{12}C$ ratio, and the trophic position of consumers, as indicated by their $^{15}N/^{14}N$ ratio (Tiunov, 2007; Potapov et al., 2019b).

Different forest ecosystems provide different microhabitats and resources that shape the vertical distribution and community composition of Collembola (Korboulewsky et al., 2021; Xie et al., 2022; Lu et al., 2025). In Central Europe, non-native Douglas fir has been widely planted due to its timber quality and the resistance to climate change. However, the effect of Douglas fir on trophic niches of Collembola compared to native European beech and Norway spruce forests remains unclear (Hobbie et al., 2007; Schmid et al., 2014; Kriegel et al., 2021). Litter and soil moisture, as main drivers of the vertical distribution of soil animals, varies between these forests (Ammer, 2019; Lwila et al., 2023), so trophic niches of Collembola are likely to differ. Thus, exploring changes in trophic niches of Collembola with soil depth and between forest types should improve our understanding of trophic niche plasticity of decomposer soil animals, and inform about the impacts of forest management on soil animal trophic ecology.

We investigated trophic niche variation in 27 Collembola species across two spatial scales, i.e. between the litter and soil layer (vertically) and across five forest types (horizontally) using bulk stable isotope analysis of ^{13}C and ^{15}N. Forest types included pure stands of European beech, Norway spruce, Douglas fir and the two conifer–beech mixtures. We hypothesized that (1) within species the trophic position of Collembola increases from the litter to the soil layer because they feed more on resources from the soil layer (pointing to vertical niche differentiation), (2) the trophic niche of Collembola species varies little between different forest types reflecting that consistent microhabitats with the same food sources are present across forest types, and (3) as Collembola mainly feed on fungi, that changes in fungal biomass between the litter and soil layer drive the differences in the trophic position of Collembola species between litter and soil.

2. Materials and methods

2.1. Sampling sites

The study was conducted in 40 forest stands across five forest types, arranged in eight quintets, representing a broad range of precipitation and soil conditions in northern Germany (Table S1, Fig. S1). Soil types were Podzol in the four northern quintets, and Cambisol and Luvisol in the southern quintets (Lu et al., 2022). Henceforth, we refer to the northern sites as sandy and to the southern sites as loamy. Each quintet included three pure forests of European beech forest, Douglas fir forest and Norway spruce, and two mixed forests of European beech either with Douglas fir or with Norway spruce. The three dominant tree species in the pure forests accounted for at least 90% of the total basal area. In mixed Douglas fir forests, focal tree species comprised on average 34% European beech and 58% Douglas fir. In mixed Norway spruce forests, focal tree species comprised on average 56% European beech and 37% Norway spruce (Ammer et al., 2020). The forests were dominated by mature trees of an average age of 80 years (Glatthorn et al., 2023). More details on site characteristics and soil chemical properties are given in Foltran et al. (2023) and Glatthorn et al. (2023).

2.2. Animal extraction

In each forest, one soil core was collected by using a soil corer (ø 20 cm) between November 2017 and January 2018. Samples were taken between the focal tree species. Soil cores were divided into litter layer (O_L) and 0–5 cm beneath this layer comprising $O_{F/H}$ and/or A_H material. Collembola were extracted by heat (Kempson et al., 1963), stored in 70% ethanol and sorted at species level (Hopkin, 2007). Further, in each forest bulk soil cores were taken including litter and 0–5 cm soil layers by using a soil corer (ø 5 cm) for bulk stable isotope analysis (Lu et al., 2022).

2.3. Species selection

Within soil cores, we selected Collembola species of different life form (epedaphic, hemiedaphic and euedaphic) occurring in both the litter and soil layers. The assignment of life forms was based on morphological traits as described in Potapov et al. (2016). In total 27 Collembola species comprising 1733 individuals were selected, with 16 species occurring in more than one forest type. Ten more Collembola samples were investigated from litter or soil to cover rare species leading to a total of 250 Collembola samples, i.e., 8 forests × 5 forest types × 2 soil depths × 3 Collembola life forms + 10 (Table S2).

2.4. Stable isotope analysis

Stable isotope values of Collembola were used to quantify their trophic niches. Depending on body size of the species, different numbers of individuals were pooled per sample to obtain an average of 20 μg dry weight. Equal numbers were used for each Collembola species from different depths of the same soil core (Table S3). Collembola were transferred into silver capsules (ø 3.3 mm × 4.0 mm) and dried at 60 °C for 48 h. Then, stable isotope ratios were measured using a coupled system of an elemental analyzer (Flash 2000; Thermo Fisher Scientific, UK) and a stable isotope mass spectrometer (Delta V Advantage, Thermo Electron, Germany). Animal samples were analyzed using a near-conventional setup developed for small sample amount (Langel and Dyckamans, 2014). Atmospheric N and Vienna PeeDee belemnite were used as primary standards for N and C stable isotopes, respectively, and acetanilide (Merck, Germany) as working standard. The ratios (δX) of C and N stable isotopes were calculated as δX (‰) = (R_{sample} - $R_{standard}$)/$R_{standard}$ x 1000, with R referring to the ratio between heavy and light stable isotopes, i.e. $^{13}C/^{12}C$ and $^{15}N/^{14}N$.

Litter and 0–5 cm soil samples from each forest were dried at 60 °C for 48 h, ground in a ball mill and then weighed into capsules. Stable isotope values of litter were used as baseline for comparing Collembola species across forest types (Klarner et al., 2013; Potapov et al., 2019b). Litter-corrected stable isotope values of Collembola are denoted with large delta (Δ).

2.5. Soil pH and microbial community composition

Soil pH was determined using a ratio of sample to solution (g/mL; KCl, 1 mol/L) of 1 : 10 for litter and 1 : 5 for soil (Lu and Scheu, 2021). The relative proportion of Gram-positive bacteria, Gram-negative bacteria and fungi as determined by phospholipid fatty acid (PLFA) analysis was used to relate trophic niches of Collembola to food resources. In short, 2 g (4 g) of fresh litter (soil) were used for the extraction of lipids by using a modified Bligh and Dyer method (Frostegård et al., 1993; Pollierer et al., 2015; Lu and Scheu, 2021). The saturated fatty acids i15:0, a15:0, i16:0 and i17:0 were used as markers for Gram-positive bacteria, and the fatty acids cy17:0, cy19:0, 16:1ω7 and 18:1ω7 were assigned as markers for Gram-negative bacteria (Zelles, 1999; Fanin et al., 2019). Linoleic acid 18:2ω6,9 was used as fungal marker (Frostegård and Bååth, 1996). Total amount of PLFAs included all identified PLFAs (nmol g^{-1} dry weight) was used to calculate PLFA proportions, for details of the measurement see Lu and Scheu (2021).

2.6. Data analysis

Linear mixed models (LMMs) were used to analyze the variation in $\delta^{15}N$ and $\delta^{13}C$ values of Collembola. Fixed effects included soil depth (litter and 0–5 cm soil), forest type (European beech, Douglas fir, Norway spruce, European beech-Douglas fir and European beech-Norway spruce), life form (epedaphic, hemidaphic and euedaphic) and site condition (sandy and loamy). Stable isotope values of litter and 0–5 cm soil were included as covariates at stand level to control for differences in the baseline across forests (Melguizo-Ruiz et al., 2017). Random effects included the 40 forests and 27 species, controlling for the non-independence of Collembola sampled from the same soil core, and for species differences. The differences in marginal estimated means of Collembola $\delta^{15}N$ and $\delta^{13}C$ values between litter and soil layers were used as depth effects on trophic niches of Collembola populations (Piovia-Scott et al., 2019).

Since the studied Collembola species are not statistically independent due to shared evolutionary history, phylogenetic covariance among species was included as random effect in Bayesian regression models (Bürkner, 2017). First, the phylogenetic tree of 27 species was built based on their 18S ribosomal DNA genes using Maximum likelihood (Fig. S2; Xiong et al., 2008; Peguero et al., 2019). *Acerentomon franzi* (Protura) and *Catajapyx aquilonaris* (Diplura) were used as outgroup, which allowed us to determine the root of Collembola species, but was removed before further analysis (Yu et al., 2024). Then, the covariance matrix of 27 species was extracted and treated as random effect in Bayesian regression models. Besides, to measure how well the phylogenetic tree explains the trait data we calculated the phylogenetic signals of $\Delta^{15}N$ and $\Delta^{13}C$ values of Collembola and trophic variation with soil layers using the variance proportions of phylogenetic relations in ‘brms’ (Losos, 2008; Revell, 2024).

To inspect environmental drivers of vertical changes in Collembola trophic position, we used structural equation models (SEMs) to test pathways linking changes in environmental conditions to changes in $\delta^{15}N$ values of Collembola between litter and soil layers. For trophic parameters, bulk $\delta^{15}N$ values, bacterial and fungal PLFAs, and the bacterial to fungal PLFA ratio were included. Soil pH was also included because of its crucial effects on soil microbial communities. For other soil properties, a correlation test was conducted between the differences of those parameters and the differences of $\delta^{15}N$ values of Collembola or microbial concentrations between litter and soil layers. Only significant ones were included in the SEMs, which included soil N content (%) and C/N ratio. All variables were scaled between 0 and 1. The effect of forest type on pathways was not included because its effect on Collembola $\delta^{15}N$ values was not significant (Table 1). Interactive pathways among microbial parameters such as fungal and bacterial biomass and their proportions were not included in the initial model (Fig. S3) but were added successively based on model selection using the modification indices (univariate score tests). No further pathways were included if the p-value of the model was larger than 0.05.

All analyses were performed with the R software (4.0.5 version, https://www.r-project.org). The data met the assumptions of normality of residuals and homogeneity of variances. The packages ‘lme4’ and ‘emmeans’ were used to fit LMMs and estimate marginal means, respectively (Bates et al., 2015). The package ‘lmerTest’ was used to estimate p-values of LMMs by Satterthwaite’s method (Kuznetsova et al., 2017). The package ‘ape’, ‘phangorn’ and ‘rentrez’ were used to run the phylogenetic tree and calculate the phylogenetic distance matrix between species (Paradis et al., 2004; Schliep, 2011; Winter, 2017). The package ‘phytools’ and ‘brms’ were used to visualize phylogenetic trees and run the Bayesian regression models, respectively (Bürkner, 2017; Revell, 2024). SEMs and the modification indices were run using the packages ‘lavaan’ and ‘semTools’, respectively.

3. Results

3.1. Isotopic niche of Collembola

The $\delta^{15}N$ and $\delta^{13}C$ values in bulk soil were consistently higher than in litter across the studied forest types, with the differences being largest in beech (3.91 and 1.70 ‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively) and smallest in Douglas fir forest (respective values of 2.45 ‰ and 0.60 ‰) (Fig. 1a). In Collembola, the $\Delta^{15}N$ but not the $\Delta^{13}C$ values were significantly

Table 1
Chi-square and P-values of liner mixed-effects models on the effects of depth (litter and 0–5 cm soil), forest type (European beech, Douglas fir, Norway spruce, European beech-Douglas fir and European beech-Norway spruce), Collembola life form (epedaphic, hemiedaphic and euedaphic), site condition (sandy and loamy) and their interactions on $\delta^{15}N$ and $\delta^{13}C$ values of Collembola species. Significant effects are given in bold (p < 0.05).

		$\delta^{15}N$		$\delta^{13}C$	
	df	Chisq	P-value	Chisq	P-value
Depth (D)	1	24.07	**<0.001**	2.23	0.135
Forest (F)	4	1.47	0.833	44.52	**<0.001**
Life form (L)	2	7.14	**0.028**	11.74	**0.003**
Site condition (S)	1	0.28	0.595	0.42	0.517
D × F	4	10.54	**0.005**	0.74	0.690
D × L	2	2.40	0.301	0.19	0.907
D × S	1	0.67	0.412	15.61	**<0.001**
F × L	8	7.56	0.477	8.95	0.346
F × S	4	1.60	0.809	3.33	0.503
L × S	2	6.21	0.184	7.02	0.135
D × F × L	8	6.73	0.566	3.52	0.897
D × F × S	4	1.56	0.816	8.61	0.072
D × L × S	2	3.07	0.215	4.14	0.126
F × L × S	8	11.06	0.198	5.42	0.712
D × F × L × S	8	4.40	0.819	5.64	0.687

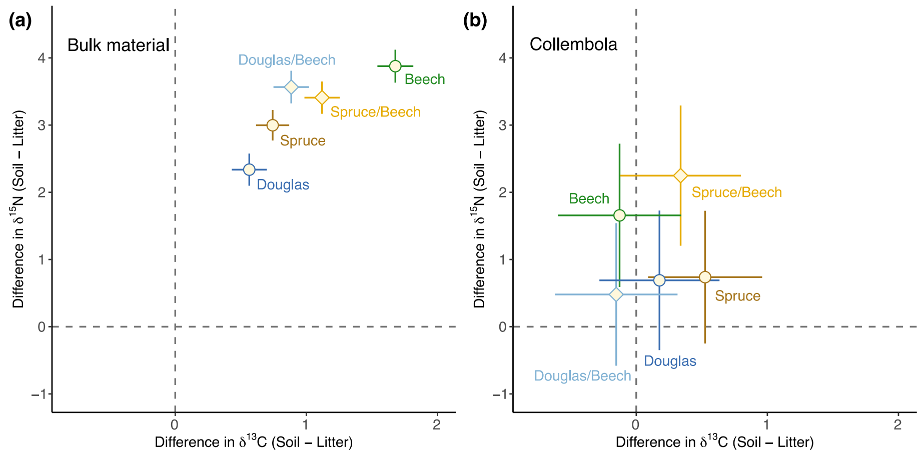

Fig. 1. Differences in δ^{15}N and δ^{13}C values of bulk material (a) and Collembola (b) between the litter and 0–5 cm soil layer of five forest types [European beech (Beech, green), Douglas fir (Douglas, blue), Norway spruce (Spruce, brown), mixed forests of Douglas fir and European beech (Douglas/Beech, light blue), mixed forests of Norway spruce and European beech (Spruce/Beech, orange)]; means ± 95% confidence intervals.

higher in soil than in litter and this varied with forest type (Table 1, S4, Fig. 2). The differences in δ^{15}N values between layers were significant in European beech (+1.62 ‰) and mixed Norway spruce forests (+1.89 ‰), but were less pronounced in Douglas fir, Norway spruce and mixed Douglas fir forests (Table 1, Fig. 1b).

Based on litter-calibrated δ^{15}N values (Δ^{15}N), 27 species of Collembola from the litter were grouped into three trophic guilds, i.e. primary decomposers, secondary decomposers and omnivores/predators (Fig. 3). Compared to Collembola in the litter layer the trophic positions of eight Collembola species shifted towards higher δ^{15}N values in the soil layer (Fig. 3b). These species included all three life-forms studied; *Sminthurinus aureus*, *Parisotoma notabilis* and *Isotomiella minor* shifted from primary decomposers to secondary decomposers, whereas *Paratullbergia callipygos*, *Frisea mirabilis*, *Neanura muscorum* and *Ceratophysela denticulata* shifted from secondary decomposers to omnivores/predators, and *Tomocerus minutus* shifted from primary decomposers to omnivores/predators (Fig. 3b).

At loamy sites, the Δ^{13}C values of Collembola were 0.52 ‰ higher in the soil than in the litter layer, whereas Δ^{13}C values of Collembola did not significantly differ between litter and soil at sandy sites (Table 1, Fig. S4). The Δ^{15}N values of Collembola generally did not significantly differ between forest types (Table 1, Fig. 4a). By contrast, the Δ^{13}C values of Collembola were significantly higher in beech forests than in mixed and pure coniferous forests (Table 1, Fig. 4a), and Δ^{13}C values of Collembola in spruce forests were 1.6 ‰ lower than in beech forests (Fig. 4a). Both Δ^{13}C and Δ^{15}N values of Collembola were higher in euedaphic than in hemidaphic and epedaphic Collembola (Table 1, Fig. 4b).

Generally, phylogenetic relationships among Collembola species more strongly affected the Δ^{15}N values of Collembola than the differences in δ^{15}N values between soil depths (i.e., $\Delta^{15}N_{soil\text{-}litter}$) (Table S5, Fig. 5). The phylogenetic relationships among species explained more variation in Δ^{15}N (79.63%) and Δ^{13}C values (86.02%) of Collembola than in differences of Δ^{15}N and Δ^{13}C values between soil depths (5.71% and 20.38%, respectively). Species belonging to Poduromorpha and Entomobryomorpha, in the phylogenetic tree from *Paranura sexpunctata* to *Tomocerus vulgaris*, generally had high Δ^{15}N and Δ^{13}C values (Fig. 5). Meanwhile, some species of Entomobryomorpha, from *Isotomiella minor* to *Lepidocyrtus lignorum*, had low Δ^{15}N values. All species generally had high $\Delta^{15}N_{soil-litter}$ values except for the three species of Poduromorpha, i.e. *Lathriopyga longiseta*, *Friesea mirabilis* and *Ceratophysella denticulata*.

3.2. Pathways affecting shifts in the trophic positions of Collembola

As indicated by SEM, the increase in Collembola δ^{15}N values from litter to soil correlated positively with the changes in the PLFA marker for Gram-positive bacteria from litter to soil, but negatively with the changes in the PLFA marker for Gram-negative bacteria (Fig. 6). The changes in soil pH and C/N ratio between litter and soil were negatively related to the changes in Gram-positive bacteria between litter and soil.

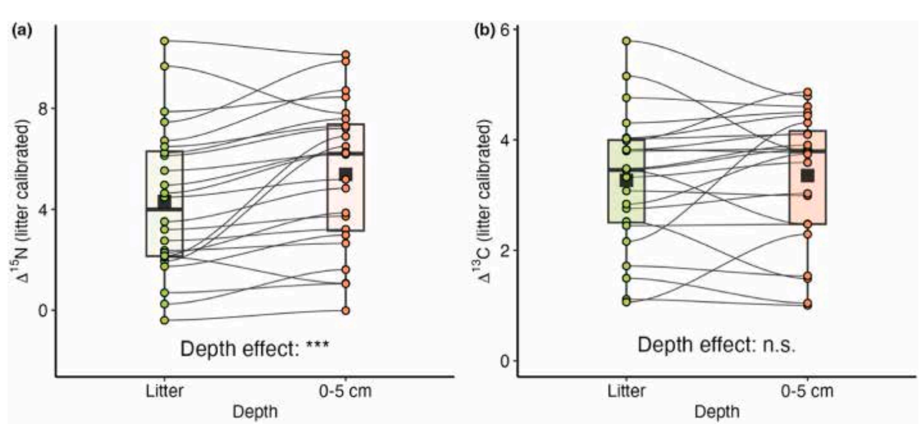

Fig. 2. Changes in Δ^{15}N (a) and Δ^{13}C (b) values of Collembola species between litter and 0–5 cm soil; points indicate mean Δ^{15}N and Δ^{13}C values of species; black squares indicate the mean value of all species in the litter or soil layer across forests (European beech, Douglas fir, Norway spruce, European beech-Douglas fir and European beech-Norway spruce), site conditions (sandy and loamy) and life forms (ep-, hemi- and euedaphic). ***: $p < 0.001$; n.s.: not significant ($p > 0.05$).

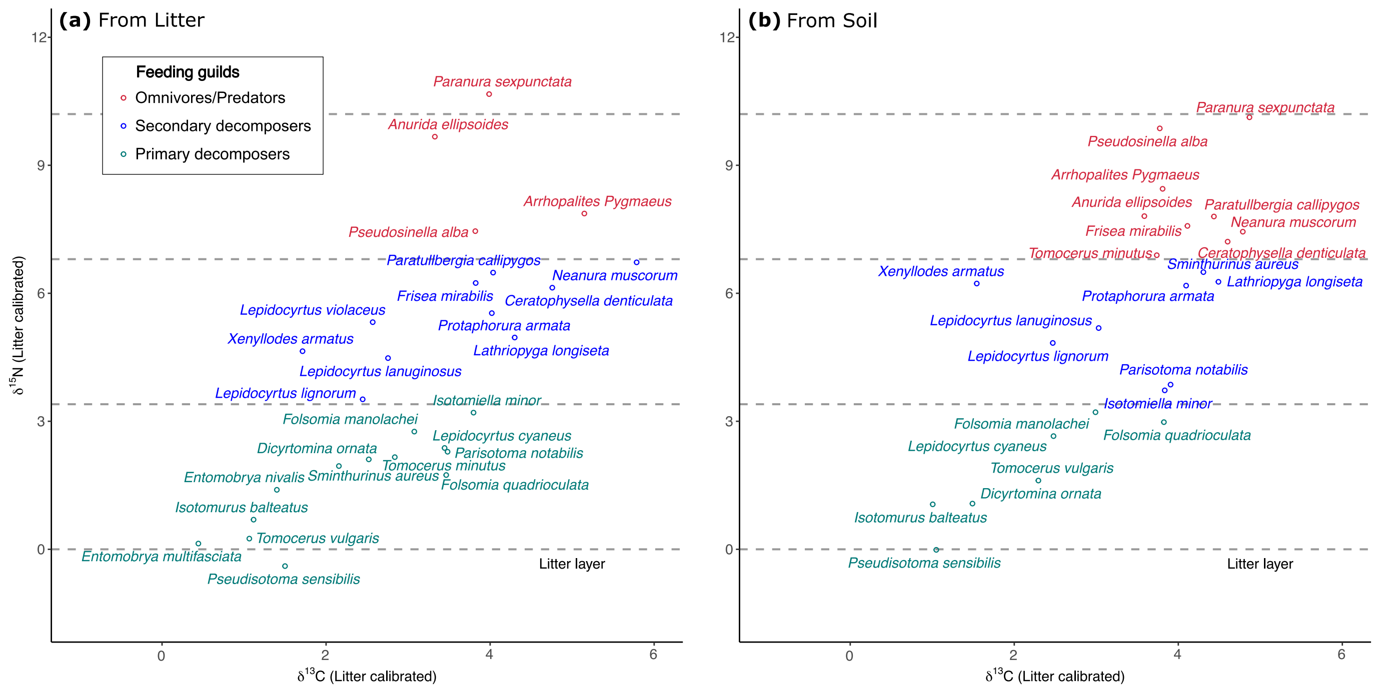

Fig. 3. Biplot of Δ^{15}N and Δ^{13}C values of Collembola species in the litter (a) and 0–5 cm soil (b) with Collembola species assigned to trophic guilds, i.e. primary decomposers (green), secondary decomposers (blue) and omnivores/predators (red); the number of replicates per species are given in Table S1.

The changes in soil N content (%) between litter and soil were positively related to the changes in Gram-positive bacteria between litter and soil. Further, larger changes in Gram-negative bacteria between litter and soil were associated by a more pronounced increase in δ^{15}N values of bulk material of litter and soil. However, changes in δ^{15}N values of bulk materials were not significantly related to changes in δ^{15}N values of Collembola species between litter and soil.

4. Discussion

Strong phylogenetic signal of Δ^{13}C and Δ^{15}N values in Collembola supports the trophic niche conservatism hypothesis (Losos, 2008; Potapov et al., 2016) and points to significant evolutionary constraints in the evolution of trophic niches in Collembola. Further, δ^{15}N values of Collembola uniformly increased from the litter to the soil layer across forest types, site conditions and taxonomic/phylogenetic groups, showing for the first time that trophic plasticity at the microscale is independent of ecosystem type and evolutionary history. This trophic shift with soil depth generally suggests increased use of microbial food resources deeper in soil. It also reflects high adaptability to changes in resource availability and composition. Notably, our SEM analyses suggest that bacteria rather than fungi, as main food resource of Collembola (Chahartaghi et al., 2005; Pollierer and Scheu, 2021), drives the changes in the trophic position of Collembola from litter to soil. Our results contrast previous observations that reported high trophic consistency of oribatid mite species between soil layers (Lu et al., 2022) suggesting Collembola have higher trophic plasticity than oribatid mites.

4.1. Change in the trophic position of Collembola from litter to soil

Within species, the δ^{15}N values of Collembola generally increased form the litter to the soil, supporting our first hypothesis. The results suggest that when Collembola move vertically, they ingest the food resources which are locally available rather than returning to the initial habitat for feeding. Previous studies found the trophic position of Collembola at community level to vary between microhabitats and ecosystem types (Fujii et al., 2023; Lux et al., 2024b), with this shift being mainly driven by intraspecific variations rather than species turnover (Lux et al., 2024b). Our results support these findings and further indicate that most Collembola species irrespective of life form are able to adapt their trophic niches, i.e. almost all species contributed to the change in the trophic niche of Collembola from litter to soil. Importantly, the uniform increase in the trophic position of Collembola species from litter to soil resulted in similar differences in trophic niches between species in litter and soil. This points to a uniform response of Collembola species to shifts in resource composition, which may help to minimize competition between species within each vertical microstratum. Our results in part contrast earlier studies reporting that ^{15}N/^{14}N ratios of Collembola species do not vary significantly with soil depth (Scheu and Falca, 2000). This difference may relate to the fact that we investigated considerably more Collembola species across a much larger number of forest sites. Therefore, for the first time we show that the trophic niche of Collembola species varies with the vertical microhabitat the species colonizes reflecting shifts in resource availability with soil depth.

Previous studies found the resource utilization of Collembola to vary between species and this forms the basis for assigning Collembola species to different trophic guilds, i.e. primary decomposers, secondary decomposers and omnivores/predators (Scheu and Falca, 2000; Chahartaghi et al., 2005; Potapov et al., 2022). In our study, the trophic position of Collembola species increased by about one third trophic level between litter and soil assuming an enrichment in ^{15}N by 3.4 ‰ per trophic level (Post, 2002; Potapov et al., 2019a). Considering the proximity of the two layers studied, this shift is large as it represents a similar shift in the trophic position of Collembola communities across an elevation gradient from 800 to 1700 m on Changbai Mountain (Lux et al., 2024b). Overall, the shift in the ^{15}N/^{14}N ratios reflects that the Collembola in the litter layer more intensively live as primary decomposers and switch to living as secondary decomposers or omnivores/predators in soil.

4.2. Tree species modify Collembola trophic niches

The δ^{13}C values of Collembola decreased from beech forests to mixed

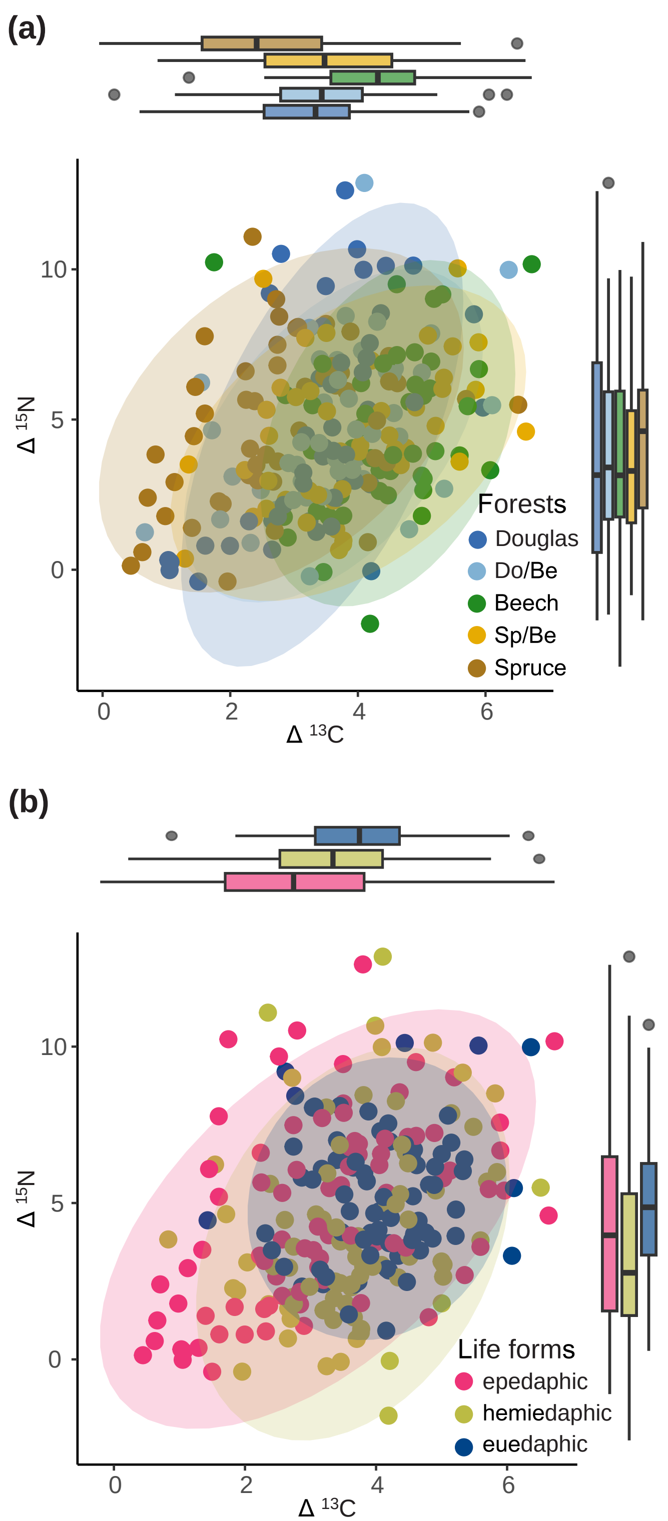

Fig. 4. Variations in Δ^{15}N and Δ^{13}C values of Collembola species between forest types (European beech, Douglas fir, Norway spruce, European beech-Douglas fir and European beech-Norway spruce) (a) and life forms (epedaphic, hemiedaphic and euedaphic) (b); ellipses represent 95% confidence intervals; in (a) the numbers of replicates are 50, 47, 46, 47 and 54 for Douglas, Dogulas/Beech, Beech, Spruce/Beech and Spruce forests, respectively; in (b) the numbers of replicates are 84, 81 and 79 for ep-, hemi- and euedaphic Collembola, respectively.

forests to coniferous forests, supporting our second hypothesis. Shifts in δ^{13}C values in Collembola between different forests have been shown before and have been related to changes in resource quality declining, e.g., from low to high elevation (Lux et al., 2024b). Similarly, differences in litter quality may also have been responsible for the differences in δ^{13}C values in Collembola in the different forest types in our study. The more pronounced shift in δ^{13}C values, i.e. the larger Δ^{13}C values (larger 'detrital shift'; Potapov et al., 2019b) in beech compared to conifer and beech – conifer mixed forests reflects the lower litter quality of beech compared to Douglas fir and spruce as indicated by higher C/N ratio of freshly fallen leaves respectively needles (50.7 vs 39.3 vs 39.8) in the former (Stuckenberg et al., 2025). However, the more pronounced shift in δ^{13}C values in Collembola in beech forests than in conifer and beech – conifer mixed forests may also be related to lower δ^{13}C values in beech litter (−29.57 ‰) than in litter of Douglas fir (−28.40 ‰) and Norway spruce forests (−28.12 ‰), thereby reflecting the calibration of Δ^{13}C values of Collembola.

In contrast to δ^{13}C values, the δ^{15}N values of Collembola did not differ significantly between forest types. The high variability in δ^{15}N values of Collembola between soil layers raises question about using it as a species trait in functional analysis of species. On the other hand, the high consistency of the trophic position of Collembola species across different forest types suggest that trophic position may serve as species trait in the analysis of Collembola communities, but this requires considering their variation across different soil layers (Lu et al., 2022, 2024, 2025). The shift in δ^{15}N values of Collembola between litter and soil was higher in beech forests and beech-spruce mixed forests than in beech-Douglas fir mixed forests indicating a more pronounced shift from primary to secondary decomposers and more intensive use of microbial resources from litter to soil in beech and beech – conifer mixed forests than in pure conifer stands. However, also other factors such as differences in soil moisture between beech and conifer stands may have contributed to the more pronounced shift in δ^{15}N values of Collembola from litter to soil in beech compared to conifer forests. Generally, the wider range of δ^{15}N values of Collembola species in mixed Norway spruce forests than in beech forests and spruce forests point towards wider niche breadth of Collembola in mixed compared to pure stands at least in spruce – beech mixed forests. Overall, the limited effect of tree species composition but the strong effects of soil depth on Collembola trophic position highlights the importance of the local resource spectrum and the vertical microhabitat in shaping the trophic niche of Collembola.

4.3. Linking Collembola trophic plasticity to shifts in the composition of microbial communities

As indicated by SEM, the increase in δ^{15}N values of Collembola from the litter to soil was not related to changes in the relative contribution of fungi to microorganisms in litter and soil (as indicated by PLFA analysis), but rather, to an increase in the relative contribution of Gram-positive and a decrease in the relative contribution of Gram-negative bacteria, arguing against our hypothesis 3. The gut content of Collembola includes pollen grains, algae, fungi and humus materials (Ponge, 2000), but little is known on the proportion of bacteria in the gut of Collembola. Collembola are assumed to mainly feed on fungi, with the proportion of bacteria to their diet being < 25%. (Pollierer and Scheu, 2021; Lux et al., 2024a). However, lipid analysis also indicates that Collembola digest more bacteria, especially the Gram-positive bacteria, than oribatid mites (Lux et al., 2024a) indicating that especially Gram-positive bacteria may play a more prominent role for the nutrition of Collembola than previously assumed. However, it remains unclear whether the increase in Collembola δ^{15}N values between in litter and soil in fact is due to more intensive digestion of Gram-positive bacteria and an increased proportion of microorganisms in their diet reflecting increased trophic inflation (Steffan et al., 2017) or if this interrelationship reflects indirect effects of Gram-positive bacteria on the digestion of

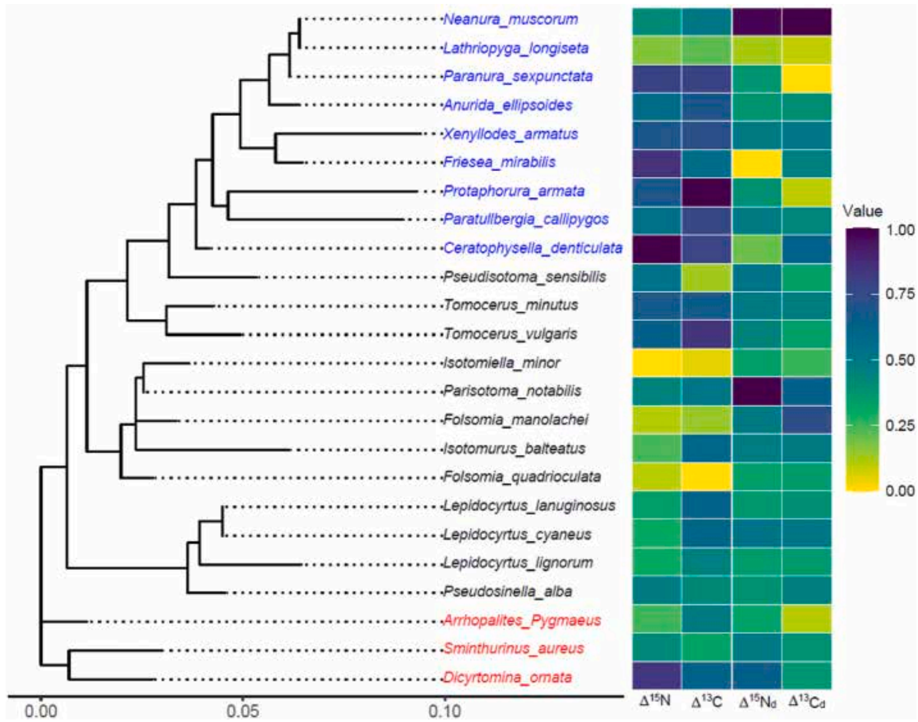

Fig. 5. Phylogenetic tree showing evolutionary relationships between the studied Collembola species, and the phylogenetic signal of trophic niches (represented by Δ^{15}N and Δ^{13}C values) and trophic plasticity, i.e. the difference between Δ^{15}N and Δ^{13}C values between litter and soil ($\Delta^{15}N_d$, $\Delta^{13}C_d$; respectively). Species trait values were scaled between 0 and 1. *Entomobrya multifasciata*, *E. nivalis* and *Lepidocyrtus violaceus* were removed from the tree because they only occurred in a single soil depth. The blue, black and red species belong to the orders of Poduromorpha, Entomobryomorpha and Symphypleona, respectively. The yellow to dark purple colors reflect the gradient from small to high values of Δ^{15}N, Δ^{13}C, $\Delta^{15}N_d$ and $\Delta^{13}C_d$, i.e. from 0 to 1.

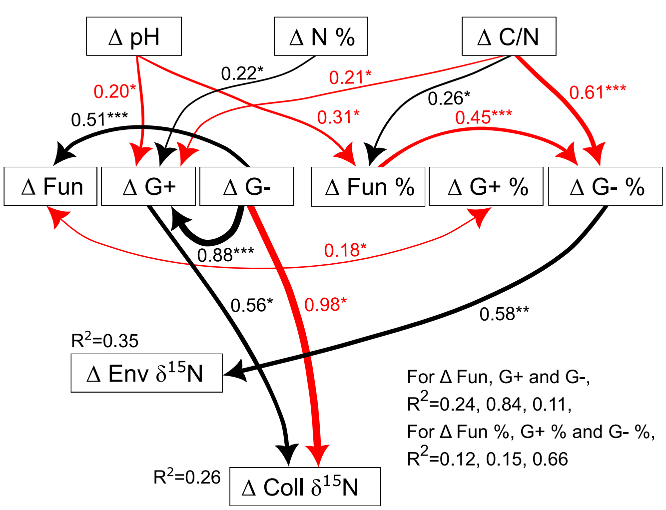

Fig. 6. Structural Equation Models (SEMs) showing the effect of soil depth (from litter to soil) on trophic position (Δ Coll δ^{15}N) of Collembola in forests as related to soil pH, soil N content (ΔN %), soil C/N ratio (Δ C/N), biomass and percentages of microbial guilds, and bulk δ^{15}N values between litter and soil (Δ Env δ^{15}N). Δ Fun, Δ G+ and Δ G- refer to the biomass of fungi, Gram-positive and Gram-negative bacteria as indicated by phospholipid fatty acids (PLFAs), respectively; Δ Fun %, Δ G+ % and Δ G- % refer to their relative proportions of total PLFAs. Model fits for the complete model: $\chi^2 = 23.56$, $p = 0.073$, df = 15, cfi = 0.960, gfi = 0.915, rmsea = 0.119, $p_{rmsea} = 0.123$. Solid and dashed gray arrows represent significant ($p < 0.05$) and non-significant ($p \geq 0.05$) relationships, respectively. Dark and red arrows represent positive and negative paths, respectively. Arrow width is proportional to standardized path coefficient. Non-standardized path coefficients associated with solid arrows are shown (***, $p < 0.001$, **, $0.001 \leq p < 0.01$, *, $0.01 \leq p < 0.05$), n = 40. Δ refers to the difference between the respective value in soil and litter.

food materials of Collembola. Also, caution is needed in interpreting the role of Gram-positive bacteria to Collembola nutrition as the increase in Collembola δ^{15}N values from litter to soil also closely correlated with a decrease in the relative contribution of Gram-negative bacteria to microorganisms from litter to soil.

5. Conclusions

For the first time we investigated variation in the trophic niches of Collembola between ecosystems (horizontal variation) and with soil depth (vertical variation). The results show that vertical variations considerably exceed horizontal variations. Low variations in trophic positions between different forest types including deciduous and coniferous species point to a remarkable constancy of trophic niches of Collembola species. However, marked vertical shifts in their trophic niches from litter to soil also point to pronounced trophic plasticity associated with changes in food resources and soil microhabitat, an ability that is common in Collembola and largely independent of their evolutionary history. The shift in trophic niches with soil depth in Collembola contrasts the invariance of trophic niches of oribatid mites with soil depth. The consistent increase in the trophic position of Collembola species with soil depth reflects more pronounced microbivory, associated with trophic inflation, in soil than in litter and stresses the importance of the microstratification of their trophic niche in space. Using structural equational modelling, we identified increased proportion of Gram-positive bacteria to microorganisms to be closely related the increase in the trophic position of Collembola from litter to soil. Overall, the results highlight the importance of the vertical microhabitat structure for trophic niches of Collembola and point to the plasticity of Collembola species to adapt their diet to locally available resources. This also points to the pronounced ability of Collembola to cope with changing environmental conditions.

CRediT authorship contribution statement

Junbo Yang: Validation, Investigation, Formal analysis, Conceptualization, Writing – review & editing, Writing – original draft, Visualization, Funding acquisition. **Gaozhong Pu:** Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Formal analysis. **Melissa Jüds:** Validation, Methodology, Investigation, Writing – review & editing. **Amandine Erktan:** Writing – review & editing, Methodology. **Stefan Scheu:** Data curation, Conceptualization, Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis. **Jing-Zhong Lu:** Supervision, Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, 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.soilbio.2025.109912.

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