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# Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis ($^{15}N/^{14}N$)

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## Abstract

We investigated if the commonly used aggregation of organisms into trophic guilds, such as detritivores and predators, in fact represent distinct trophic levels. Soil arthropods of a forest-meadow transect were ascribed *a priori* to trophic guilds (herbivores, detritivores, predators and necrovores), which are often used as an equivalent to trophic levels. We analysed natural variations in $^{15}N/^{14}N$ ratios of the animals in order to investigate the trophic similarity of organisms within (*a priori* defined) trophic guilds. Using trophic guilds as an equivalent to trophic level, the assumed stepwise enrichment of $^{15}N$ by 3.4‰ per trophic level did not apply to detritivores; they were only enriched in $^{15}N$ by on average 1.5‰ compared to litter materials. Predators on average were enriched in $^{15}N$ by 3.5‰ compared to detritivores. Within detritvores and predators $\delta^{15}N$ signatures varied markedly, indicating that these trophic guilds are dominated by generalist feeders which form a gradient of organisms feeding on different resources. The results indicate that commonly used trophic guilds, in particular detritivores and predators, do not represent trophic levels but consist of subguilds, i.e. subsets of organisms differing in resource utilization. In particular, in soil and litter food webs where trophic level omnivory is common, the use of distinct trophic levels may be inappropriate. Guilds of species delineated by natural variations of stable isotope ratios are assumed to more adequately represent the structure of litter and soil food webs allowing a more detailed understanding of their functioning.

**Keywords:** soil animal community, trophic level, $^{15}N$, trophic level enrichment, detritivores, predators

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## Introduction

Trophic links in food web studies often are hierarchically structured according to distinct trophic levels (Hunt *et al*., 1987; Schaefer, 1990; De Ruiter *et al*., 1996; Zheng *et al*., 1997; Bengtsson *et al*., 1998). Trophic levels usually are assumed to consist of animal guilds feeding on similar resources with the distance of adjacent levels being equivalent to that between a consumer and its resource. In terrestrial animal communities, consumers feeding on dead organic matter are usually aggregated to detritivores and those feeding on living plant material to herbivores. Consumers feeding on living animal tissue are aggregated to predators and those feeding on dead animals to necrovores. These trophic guilds often are used as equivalents to trophic levels.

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Ascribing species to trophic levels is particularly difficult in soil animal communities in which generalist opportunistic feeders and trophic level omnivores predominate (Scheu, 2002; Scheu & Setälä, 2002). In terrestrial ecosystems, a substantial part of primary production enters the detritus food web (Polis, 1991; Hairston & Hairston, 1993; Coleman & Crossley, 1996). Primary decomposers, such as fungi and bacteria, dissipate most of the detritus bound energy. Abundant decomposing arthropods, such as Collembola and Diptera, are considered to predominantly feed on fungi gaining energy out of detritus associated microorganisms (Schaefer, 1991). The diet of detritivores includes detrital materials originating from all trophic levels of the food web, i.e. plant and animal tissues, bacteria, algae and fungi. Detritivores differently use this heterogeneous pool of resources; and, as a consequence, the trophic guild of detritivores consists of subguilds of species forming a gradient of increasing trophic position spanning over more than one trophic level. The same likely is true for epigeic predators hunting on the soil surface, such as lycosid spiders, carabid and staphylinid beetles, for which detritivorous arthropods are an important food resource (Swift *et al*., 1979; Eisenbeis & Wichard, 1985; Nyffeler *et al*., 1994; Halaj & Wise, 2002). The trophic guild of predators in detritus-based food webs may consist of trophic subguilds differing in the relative contribution of detritivores, herbivores and predators to their diet. Further, feeding on different subguilds of detritivores or different amounts of intraguild prey or plant material suggests the existence of trophic subguilds within predators.

Besides trophic niche separation among generalist feeders, switching between resources reinforces the difficulty to assign generalist feeders to trophic levels. Also, generalist feeding results in a wide spectrum of potential interactions, which often are not adequately represented in food web models (Polis *et al*., 1989). There is growing evidence that the concept of distinct trophic levels may not apply to soil animal communities in which generalist feeders predominate (Ponsard & Arditi, 2000; Scheu & Falca, 2000; Scheu, 2002). For this reason, it has been suggested to abandon the trophic level concept (Polis & Strong, 1996). In particular, detritivores and predators in soil likely consist of different trophic guilds spanning over more than one trophic level. A similar problem exists in taking taxonomic groups, such as spiders, as an equivalent of trophic species.

The analysis of natural variations in stable isotope ratios of nitrogen in animal tissue is increasingly used to analyse the structure of soil food webs (Ponsard & Arditi, 2000; Scheu & Falca, 2000; McNabb *et al*., 2001; Schmidt *et al*., 2004; Albers *et al*., 2006). The method is based on the assumption of constant $^{15}N$ enrichment per trophic level by 3.4‰, which has been established by analysing aquatic and above-ground terrestrial food chains (Minagawa & Wada, 1984; Post, 2002). At present, there is only little experimental evidence whether the factor of 3.4 δunits is also true for soil invertebrates. As stressed by Gannes *et al*. (1997) and Vanderklift & Ponsard (2003) the fractionation in $^{15}N$ per trophic level may not be constant. Enrichment in $^{15}N$ appears to be higher in predators feeding on protein rich diets than in herbivores living on low nitrogen food (Vanderklift & Ponsard, 2003). Low enrichment may also apply to detritivores, but there is little evidence whether this is true (Ponsard & Arditi, 2000; Scheu & Falca, 2000; Vanderklift & Ponsard, 2003).

The present study uses the stable isotope methodology to test if aggregation of organisms into trophic guilds, such as detritivores and predators, in fact represent groups of trophic similarity. We tested if fractionation of $^{15}N$ in detritivores is different from the postulated 3.4‰ (Minagawa & Wada, 1984), assuming that the enrichment in $^{15}N$ in consumers depends on nitrogen content of their resources. We hypothesised that food webs with high degrees of omnivory and opportunistic feeding consist of a gradient of organisms consuming different subsets of resources. Therefore, we expected both detritivores and predators to consist of trophic subguilds forming a gradient of increasing trophic position rather than distinct trophic levels.

## Materials and methods

The arthropod community of a forest-meadow transect in the Kranichsteiner Wald near Darmstadt (Hessen, Germany) was studied. The transect studied included a forest site, a meadow site and the transition area (distance between sites 20–40 m). Ten open pitfall traps were placed in each of the sites at a distance of 5 m from the next. Pitfall traps constituted of glass jars of a height of 12 cm and a diameter of 5.5 cm. The traps were evenly connected to the soil surface by a plastic ring and filled with *ca*. 50 ml of a 1 : 1 glycerol-water solution.

From May to October 2001 and from March to April 2002, the traps were operated for a period of two weeks at monthly intervals. Animals caught were transferred into 70% alcohol and stored until determination and counting. The $^{15}N$ content of dominant arthropod species was analysed. Dominance estimates were based on numbers of arthropods per catch.

Selection of arthropods for stable isotope analysis was based on three criteria: (i) we selected arthropods out of each of the trophic groups (detritivores, herbivores, predators, necrovores); (ii) we selected species which we expected to be linked by predator – prey interactions (e.g. collembolans and spiders); and (iii) we restricted the analysis to species which allowed replicated analysis of stable isotope ratios.

### *Preparation of samples*

Litter materials and animals were dried at 60°C and then ground with a mortar and pestle. Between 0.24 and 1.57 mg of animal tissue and about 4 mg of litter material were placed in 8 × 5 mm tin capsules. In large species (*ca*. > 0.5 mg body weight), one individual was used per sample; whereas, in small species (< 0.5 mg body weight), several individuals had to be combined. For each species, three replicates were analysed, except for some species which were replicated only twice. Isotope ratios were determined by a coupled system of an elemental analyser (NA 1500, Carlo Erba, Milan) and a mass spectrometer (MAT 251, Finnigan: Reineking *et al*., 1993). The stable isotope composition of $^{15}N$ ($\delta^{15}N$) was calculated as $\delta^{15}N = ((R_{sample}/R_{standard}) - 1) \times 1000$, where $R_{sample}$ is the $^{15}N/^{14}N$ ratio of the sample and $R_{standard}$ is the respective ratio of the standard (Peterson & Fry, 1987). Atmospheric nitrogen served as primary standard and acetanilid ($C_8H_9NO$, Merck, Darmstadt) for internal calibration.

### *Calculations and statistical analysis*

Litter material was assumed to represent the base of the food web. In order to test the usually assumed stepwise

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enrichment in $^{15}N$ per trophic level by 3.4‰, animals were ascribed *a priori* to trophic guilds (detritivores, herbivores, predators, necrovores) commonly used as an equivalent to trophic levels. The assignment was based on published data on the diet of the taxa (Locket & Millidge, 1951; Freude *et al*., 1976; Fjellberg, 1980; Zahradnik, 1985; Jones, 1990; Heimer & Nentwig, 1991; Schaefer, 1992; Chinery, 1993; Roberts, 1995; Wachmann *et al*., 1995; Sauer, 1996, 1998; Dücker *et al*., 1997; Harde & Severa, 1998; Witt, 1998). We tested if the $\delta^{15}N$ signatures differ between the *a priori* defined trophic guilds by using analysis of variance (ANOVA). Tukey's honestly significant difference test (equal sample size) or Scheffè test (unequal sample size) were used for comparison of means. For estimating the width of trophic guilds, we used the difference between maximum and minimum $\delta^{15}N$ signature of the species.

For aggregating species into trophically homogeneous subgroups, we calculated statistically homogeneous subsets of $\delta^{15}N$ signatures. For this, we used analysis of variance (ANOVA) with $\delta^{15}N$ signatures as dependent and species as independent factor. Homogeneous subgroups were calculated using Scheffé test.

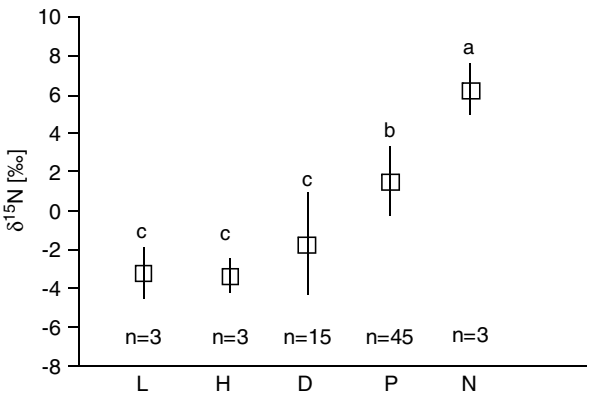


Fig. 1. Mean $\delta^{15}N$ signatures (±SD) of litter (L), herbivores (H), detritivores (D), predators (P) and necrovores (N) in a forest-meadow transect. *n*, the number of species representing this group. Significant differences are represented by different letters (Tukey's HSD test, $P < 0.05$). For aggregation of taxa, see Appendix.

## Results

### *Selection of organisms for analysis of stable isotope ratios*

Among herbivores, only Cicadellidae (mainly juvenile stages) and Delphacidae were caught in numbers allowing replicated analysis of stable isotopes.

Detritivores analyzed covered the full range of detritivore taxa with a focus on Collembola since they were most abundant and presumably of particular importance as prey for predators such as spiders. Among Collembola, we focussed on Entomobryidae, the most abundant group (72% of total). Large decomposers were represented by Diplopoda and Isopoda. Further, we analysed Diptera species (Drosophilidae, Sciaridae, Cecidomyiidae, Phoridae) since, as larvae, many of them live in soil but, as adults, may form a substantial part of the diet of aboveground predators. Other detritivores were included due to their omnipresence.

Among predators, we focussed on generalist predators, which are assumed to consume herbivorous and detritivorous prey, i.e. predaceous beetles and spiders. In spiders, we analysed each species caught, in numbers allowing replicated analysis of stable isotopes. More than 80% of the spiders were free-hunting taxa, in particular Lycosidae. In this group, we differentiated adult and juvenile stages. In Coleoptera, we focussed on Staphylinidae and Carabidae. Scydmaenidae and Dytiscidae were included due to their high numbers. Other generalist predators, which were often caught and, therefore, included in the analysis, were Erythraeidae, Phalangiidae, Nemastomatidae, Neobisiidae, Lithobiidae and Asilidae.

At the study site, three necrovores belonging to Sarcophagidae (Diptera), Silphidae and Catopidae (Coleoptera) were caught in high numbers and, therefore, included in the analysis.

### A priori *defined trophic guilds*

Epigeic soil arthropods of the studied forest-meadow transect were dominated by detritivores (80.5% of total sample) and predators (16.0%). Herbivores and necrovores represented 1.4% and 0.7% of total arthropods, respectively. We disregarded the remaining 1.4% of total arthropods (including, e.g. Geotrupidae and Gryllotalpidae), as these unlikely contribute substantially to predator nutrition. Signatures of $\delta^{15}N$ of arthropods spanned over 12.6 δunits, ranging from –5.4‰ (*Orchesella flavescens*, Entomobryidae, Collembola) to 7.2‰ (Sarcophagidae, Diptera).

Mean $\delta^{15}N$ signatures of basal resources (litter) and trophic guilds (detritivores, herbivores, predators, necrovores) differed significantly (ANOVA: $F_{4,244} = 50.07$; $P < 0.0001$). Litter materials, herbivores and detritivores had lowest $\delta^{15}N$ signatures, with the mean $\delta^{15}N$ signatures of litter materials being similar to those of herbivores and detritivores. Detritivores as trophic guild were enriched in $^{15}N$ compared to litter by on average 1.5‰. Predators were significantly enriched in $^{15}N$ compared to litter, herbivores and detritivores, compared to herbivores and detritivores by 5.0‰ and 3.3‰, respectively. Necrovores had highest $^{15}N$ signatures, being significantly enriched in $^{15}N$ compared to predators, herbivores and detritivores (fig. 1).

### *Separation of* a priori *defined trophic guilds into subguilds*

Signatures of $\delta^{15}N$ within *a priori* defined trophic guilds of detritivores and predators varied strongly, indicating that they spread over more than one trophic level. Within detritivores, signatures of $\delta^{15}N$ varied by 8.3‰ and within predators by 6.1‰. Species of both detritivores and predators formed gradients differing in $\delta^{15}N$ signatures (fig. 1).

Signatures of $\delta^{15}N$ of species differed significantly (ANOVA: $F_{71,177} = 20.37$; $P < 0.0001$). According to the Scheffé test, detritivores were separated into seven (D1–D7), herbivores into three (H1–H3), predators into four (P1–P4), and necrovores into three (N1–N3) subguilds. For species composition of subguilds, see Appendix.

### *Trophic subguilds of detritivores and predators*

Detritivore subguilds D1, D2 and D3 were depleted in $^{15}N$ compared to litter $^{15}N$ (Appendix). Signatures of $\delta^{15}N$ of detritivores D4 were similar to those of the mean litter $^{15}N$

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and detritivores D5, D6 and D7 were enriched in $^{15}N$ compared to mean litter $^{15}N$.

Predators P1 were enriched in $^{15}N$ compared to detritivores D1–D4 and to herbivores H1–H3 but depleted compared to detritivores D6–D7. Signatures of $\delta^{15}N$ of predators P1 resembled those of detritivores D5 (Appendix). Predators P2 were enriched in $^{15}N$ compared to detritivores D1–D6 and to herbivores H1–H3, but depleted compared to detritivores D7. Predators P3 and P4 were enriched in $^{15}N$ compared to each of the detritivore and herbivore subguilds and also to predators P1 and P2.

Both detritivore and predator subguilds included taxonomically similar species. Collembola were distributed among detritivore subguilds D1, D2 and D5 (Appendix); Diplopoda were included in D2, D3, D4 and D5. Within Glomeridae different developmental stages were distributed over different detritivore subguilds. Isopoda were spread over D5 and D6. As in detritivores, different predator subguilds also included taxonomical similar species. Carabid beetles were distributed over P1, P2 and P3 and spiders over P2, P3 and P4. Within spiders, different taxa of Lycosidae and even different developmental stages of two lycosid species (*T. terricola* and *P. pullata*) were distributed among different predator subguilds.

## Discussion

### *Trophic guilds*

The epigeic animal community of the forest-meadow transect investigated in this study was dominated by detritivorous and predatory arthropods; compared to these groups, herbivores were rare. This suggests that the predominant pathway of the flux of energy is from litter material to detritivores to predators. Based on the dominance of decomposers, litter material was assumed to represent the base of the food web (see also Oelbermann *et al*., 2008). Treated as trophic guild, detritivores in the present study were only enriched in $\delta^{15}N$ by, on average, 1.5‰ compared to litter material. As hypothesised before (Ponsard & Arditi, 2000; Scheu & Falca, 2000), the postulated trophic level enrichment in $\delta^{15}N$ by 3.4‰ does not apply to detritivores. Reviewing $^{15}N$ enrichment in food chains, Vanderklift & Ponsard (2003) calculated a mean $\delta^{15}N$ enrichment of only 0.5 for detritivores. Compared to detritivores, predators were enriched in $^{15}N$ by on average 3.5‰. This supports our assumption that predators of the animal community studied predominantly feed on prey out of the decomposer system.

Detritus-based food webs are characterized by heterogeneous basal resources; resources in the detritus system originate from the whole trophic spectrum in the food web, including plant and animal residues but also living microorganisms and residues of them. Leaf litter and associated microorganisms, i.e. fungi, bacteria and algae, are important resources of detritivorous arthropods. Since the diet of omnivorous feeders consists of different resources, $\delta^{15}N$ signatures of consumers may differ depending on the resource composition of their diet. Trophic level omnivory, i.e. feeding on resources of different trophic levels, is likely to result in high variations in $^{15}N$ signatures at the group and individual level. In fact, in the present study, $\delta^{15}N$ signatures varied strongly within detritivores and predators, which are commonly treated as single trophic levels. Signatures of $\delta^{15}N$ of detritivorous arthropods varied by about 8‰ and those of predatory arthropods by about 6‰, indicating different use of food resources among guild members, presumably out of different trophic levels. High variations in $\delta^{15}N$ signatures further indicate that species of the trophic guilds do not form homogeneous feeding groups or distinct trophic levels. According to the Scheffé test, the taxa studied consisted of subsets of species with statistically homogeneous $\delta^{15}N$ signatures. Trophic groups of detritivores, herbivores, predators and necrovores were distributed over different subsets, indicating the existence of trophic subguilds.

### *Delineation of trophic subgroups within trophic guilds*

Detritivores and predators consisted of species forming a gradient in $\delta^{15}N$ signatures. Treated as trophic guilds, detritivores and predators overlapped in their trophic position within the soil animal community. Based on statistically homogeneous groups, seven and four subguilds of detritivores and predators, respectively, were distinguished. Subguilds may represent functional groups within trophic guilds, reflecting gradual differences in resource combinations.

#### *Detritivores*

Differing $\delta^{15}N$ signatures of detritivores may be due to preferential consumption of habitat specific litter, litter material in different stages of decay or specific litter compartments (Tayasu, 1998; Scheu & Falca, 2000; Pollierer *et al*., 2009). Feeding on habitat specific litter may explain variability in $\delta^{15}N$ signatures by about 3 δunits. Litter of the forest was depleted in $^{15}N$ compared to litter of the meadow and the boundary area (Appendix). Preferential consumption of litter of different stages of decay may contribute to high variance of $\delta^{15}N$ signatures among detritivorous species. Compared to fresh litter, decaying litter is enriched in $^{15}N$ (Nadelhoffer & Fry, 1988; Wedin *et al*., 1995; Handley & Scrimgeour, 1997). With progressing decay of litter, the amount of associated microorganisms increases. Microorganisms are known to translocate N into decaying litter (Handley & Scrimgeour, 1997; Schimel & Hättenschwiler, 2007).

Signatures of $\delta^{15}N$ of detritivore subguilds D1–D3 were depleted in $^{15}N$ compared to mean litter $\delta^{15}N$, and those of detritivore subguild D4 differed little from those of litter. D1–D4 detritivores presumably were limited by nitrogen; however, depletion or low enrichment in $^{15}N$ may also have resulted from feeding on litter compounds low in $^{15}N$. Animals consuming low protein diets recycle rather than excrete nitrogen and synthesize new amino acids out of nitrogen of desaminated proteins (Fisler *et al*., 1982). Presumably, high nitrogen use efficiency is an adaptation of organisms which consume resources of low nitrogen concentration (Vanderklift & Ponsard, 2003). Nitrogen limited organisms have to maximize assimilation of nitrogen in food resources, i.e. decrease nitrogen excretion. Since nitrogen waste products are depleted in $^{15}N$ compared to animal tissues (Steele & Daniel, 1978), reduced excretion of nitrogen results in lower $^{15}N$ fractionation. This applies to phloem-sucking aphids (Ostrom *et al*., 1997; Yoneyama *et al*., 1997) and, presumably, also to detritivores that rely on fresh litter resources.

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Compared to litter, D5 and D6 detritivores were enriched in $^{15}N$. D5 and D6 detritivores may represent species, which increasingly gain their energy from microorganisms associated with decaying litter. Digestion of both plant material and microorganisms may facilitate nitrogen uptake by detritivores and, therefore, increase $^{15}N$ fractionation. Detritivores of subguild D7 were strongly enriched in $^{15}N$ compared to litter, indicating that they consume high amounts of animal tissue, either as predators or as necrovores. Overall, the results indicate that the postulated $^{15}N$ discrimination in detritivores depends on nitrogen uptake, which in turn depends on the association of micoroorganisms with litter. Signatures of $\delta^{15}N$ of some detritivores corresponded to those of predators. Therefore, detritivores, as commonly defined, may include species which predominantly live on a diet of animal tissue.

In the present study, Collembola dominated detritivorous arthropods. Most Collembola taxa are sapro- and microphageous (Zachariae, 1963; Wallwork, 1976; Wolters, 1985; Verhoef *et al*., 1988; Chen *et al*., 1996; Zettel *et al*., 2002), but their food spectrum also contains other soil arthropods, carcasses, bacteria, fungi and faeces of, for example, Diplopoda (Rusek, 1998), resulting in very different $\delta^{15}N$ signatures (Chahartaghi *et al*., 2005).

The Collembola investigated in the present study predominantly live on the soil surface. Signatures of $\delta^{15}N$ of Entomobryidae (D1, D2 and D5) varied by 4‰, with *Lepidocyrtus* sp. having the highest $\delta^{15}N$ signature. Signatures of $\delta^{15}N$ of each of the Collembola studied resembled that of the litter in their favoured habitat. Since litter of the meadow was enriched in $^{15}N$ compared to litter of the forest, variances in $\delta^{15}N$ signatures within Entomobryidae are likely due to the consumption of habitat specific litter with *T. longicornis* and *O. flavescens* feeding on forest litter and *Lepidocyrtus* sp. feeding on meadow litter.

Diplopoda also are known to feed on litter materials (Striganova, 1967; Blower, 1985; Eisenbeis & Wichard, 1985; Werner & Dindal, 1987; Hopkin & Read, 1992) but spread over four trophic subguilds (D2, D3, D4 and D5). Diplopoda predominantly occurred at the boundary area. Therefore, consumption of litter at later stages of decay, or coprophagy, may have contributed to variances in their $\delta^{15}N$ signatures. Signatures of $\delta^{15}N$ of *Allajulus* sp. (D2) were similar to those of forest litter but varied strongly, suggesting a broad food spectrum. Compared to *Allajulus* sp., *Glomeris* sp. (D3 and D5) and Macrosternodesmidae (D4) were enriched in $^{15}N$. Juvenile stages of *Glomeris* sp. (D5) were more enriched in $^{15}N$ than adults (D3) with their $\delta^{15}N$ signatures varying only little, suggesting narrow food spectrum. As indicated by $^{15}N$ enrichment in juvenile *Glomeris* sp., they presumably rely more on decayed litter material than adults. This might be due to small body size and weaker mandibles since litter tissue becomes softer and enriched with nitrogen with colonization by fungi. This assumption is supported by highest activity density of juvenile *Glomeris* sp. in June and July when decayed litter from the last autumn predominates.

Isopoda (D5 and D6) consume fresh and decaying litter but also reingest faeces (Striganova, 1967; Dunger, 1983; Eisenbeis & Wichard, 1985), which is known to be a common strategy of isopods to improve their nitrogen supply. In the period from May to August, isopods presumably predominantly fed on decomposed leaf litter of the previous year. As in Diplopoda, differences in $\delta^{15}N$ signatures of Isopoda may be due to varying amounts of decayed litter or coprophagy.

Low variance in $\delta^{15}N$ signatures of Drosophilidae (D6) may be related to feeding on liquids of decaying organic materials. Larvae of Sciaridae (D6) are important decomposers of litter, particularly in forests (Hövemeyer, 1999). Signatures of $\delta^{15}N$ of Sciaridae indicate that they consume a mixture of decaying litter and associated microorganisms.

Cecidomyiidae and Phoridae (D7) were enriched in $^{15}N$ by 6.0‰ compared to litter $^{15}N$. Presumably, those detritivores predominantly feed on animal tissue, either as predators or as necrovores. In fact, larvae of Cecidomyiidae have been proposed to live as predators, while adults predominantly feed on fungi (Honomichl, 1998). High $\delta^{15}N$ signatures of Cecidomyiidae, therefore, indicate that the predaceous larval phase determines the $\delta^{15}N$ signature of adults. Phoridae are adapted to live in and on the leaf litter layer, with larvae in part living endoparasitic in insects and adults, visiting flowers but in part also feeding on animal prey and carcasses (Honomichl, 1998). High $\delta^{15}N$ signatures of Phoridae indicate them to be mainly necrovorous.

Overall, detritivores presumably consist of three trophic levels with the species forming a gradient from the first to the third: (i) primary decomposers feeding on fresh litter and certain litter compounds; (ii) secondary decomposers predominantly feeding on litter associated microorganisms; and (iii) species predominantly feeding on animal tissue (predators or necrovores).

### *Predators*

As in detritivores, high variance in $\delta^{15}N$ signatures in *a priori* defined predator species indicate marked differences in food resources of predators. Predators did not form a distinct trophic level; rather, they consisted of subguilds of similar $\delta^{15}N$ signatures. Most of the predators studied are generalist feeders, hunting on the soil surface. Due to their high abundance, detritivores (81% of the captured individuals) likely formed important prey, which is also indicated by $\delta^{15}N$ signatures. Compared to detritivores, nitrogen uptake is more balanced in predators; and, therefore, discrimination of $^{15}N$ increases at higher trophic levels (Pearson *et al*., 2003). Further, $^{15}N$ fractionation presumably varies little in predators and is conform to the postulated $^{15}N$ enrichment of 3.4‰ (Minagawa & Wada, 1984; Post, 2002). Variances in $\delta^{15}N$ signatures of predators may be due to preferential consumption of a specific subguild of detritivores, to different amounts of intraguild prey or plant material in the food spectrum.

Predators consisted of four trophically homogeneous subguilds. Presumably, predators P1 predominantly feed on primary decomposers, as, compared to these, they were enriched in $^{15}N$ by 3.4‰. Signatures of $\delta^{15}N$ of predators P2 indicate that they may consume mainly secondary decomposers (D4, $\triangle = 3.8$‰), which rely on microorganisms associated with litter material and/or herbivores (H2, $\triangle =$ 3.7‰ and H3, $\triangle = 3.5$‰). As indicated by low $\delta^{15}N$ signatures intraguild predation and cannibalism are likely of minor importance. The prey spectrum of predators P3 presumably consists in large part of secondary decomposers (D6, $\triangle = 3.7$‰). Intraguild predation and cannibalism likely becomes increasingly important from predators P3 to P4. Predators P4 may consume predominantly intraguild prey (P2, $\triangle = 3.1$‰). Overall, the predator community studied appear to consist of trophic subguilds differing in the

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relative contribution of detritivores, herbivores and predators to their food spectrum.

Most of the spiders studied are mobile hunters feeding in both the meadow and forest. Spiders of the study site were distributed among different predator subguilds; they belonged to predators P2–P4. Signatures of $\delta^{15}N$ of P2 spiders indicate that intraguild predation is of little importance in these species. *Z. spinimana* hunts in the leaf litter layer and, likely, predominantly feeds on detritivores, such as Collembola. Supporting this suggestion, *Z. spinimana* was enriched in $^{15}N$ by 3.4‰ compared to *T. longicornis* and by 4.1‰ compared to *O. flavescens*. *E. frontalis* hunts in lower vegetation and *O. praticola* in higher vegetation (Roberts, 1995), suggesting they feed on herbivores. Indeed, both spider species were enriched in $^{15}N$ by *ca*. 3‰ compared to *Muellerianella* sp. and *J. pseudocellaris*, which were the dominating herbivores at the sampling site.

Results of our study suggest that differences in $\delta^{15}N$ signatures of spiders are not related to hunting strategies. Agelenid spiders use webs on the soil surface to catch their prey and, consequently, are tied to the place of their web; in contrast, lycosid and gnaphosid spiders actively hunt on the soil surface. Thomisid and pisaurid spiders hunt actively in the lower vegetation (Roberts, 1995). Despite different hunting strategies of agelenid and lycosid spiders, $\delta^{15}N$ signatures of *P. lugubris* and *H. torpida* were similar, indicating that the prey spectra of these spiders overlap; and, therefore, they may compete for prey. Although hunting strategies of lycosid and gnaphosid spiders are similar, $\delta^{15}N$ signatures differed significantly, indicating differences in the relative contribution of detritivores, herbivores and predators to their food spectrum. Interestingly, $\delta^{15}N$ signatures also differed between developmental stages of lycosid species, indicating changes in the food spectrum with age and body size.

Consistent with the assumption that the trophic position of predators scales with body size, $\delta^{15}N$ signature was at a maximum in *D. fimbriatus*, the biggest spider studied, suggesting that this species was the most vigorous intraguild predator. In a closely related species, *D. triton*, every developmental stage is known to be cannibalistic (Zimmermann & Spence, 1989). However, the trophic position of spiders did not scale uniformly with body size, e.g. $\delta^{15}N$ signature of the small species *P. degeeri* also was high, suggesting that intraguild predation also is important in smaller species.

As in spiders, $\delta^{15}N$ signatures of carabid beetles varied strongly, suggesting that they feed on very different prey. Larvae and adults of carabid beetles are predominantly predaceous. *N. biguttatus*, *Amara* sp. and *Leistus* sp. showed the postulated trophic level enrichment in $^{15}N$ compared to the Collembola species studied, indicating that they predominantly feed on Collembola. Supporting this suggestion, *N. biguttatus* hunts predominantly Collembola, including surface living species such as *Orchesella cincta* and *Tomocerus minor* (Ernsting, 1977; Ernsting *et al*., 1992). Sunderland (1975) demonstrated, that Collembola contribute 78% to the total prey of *N. biguttatus*. Also, *Leistus* sp. is known to predominantly feed on Collembola (Honomichl, 1998). Some of the carabid species studied, such as *Pterostichus* spp., *Harpalus* spp. and *Carabus* spp., are known to also live on plant resources (Sunderland, 1975; Honomichl, 1998). As indicated by the high intraspecific variation in $\delta^{15}N$ signatures, especially *Harpalus* spp. may regularly consume plant materials. *Poecilus* sp. and *D. globosus* were the carabid beetles with the highest $\delta^{15}N$ signatures. *Dyschirius* species are very small, live in the soil and consume predominantly staphylinid beetles and Heteroceridae (Eisenbeis & Wichard, 1985). *D. globosus* preferably consumes Enchytraeidae (Honomichl, 1998), which were not analysed in this study but have been shown to be rather enriched in $^{15}N$ (by ~4‰ compared to plant residues: Albers *et al*., 2006).

Despite sharing the same habitat, adult staphylinid beetles (P2) were depleted in $^{15}N$ compared to larvae (P3), indicating that intraguild predation is more important in larvae than in adults. Signatures of $\delta^{15}N$ of the adult staphylinid beetle species studied were similar, indicating consumption of prey of similar trophic position. In some staphylinid beetles, Collembola and aphids form important prey as, for example, in *Stenus* spp. (Sunderland *et al*., 1987; Honomichl, 1998). In our study, *Stenus* spp. was enriched in $^{15}N$ by *ca*. 5.7‰ compared to Collembola, suggesting that they also consume detritivores of higher trophic position and/or intraguild prey.

The analysis of stable isotopes of nitrogen is a powerful tool to depict the structure of food webs predominated by generalist feeders (Schmidt *et al*., 1997; Tayasu *et al*., 1997; Neilson *et al*., 1998; Briones *et al*., 1999; McNabb *et al*., 2001; Oelbermann *et al*., 2008). Further, the method, as applied in the present study, may allow depicting interactions within trophic levels. However, until today, only little was known about the pattern of $^{15}N$ enrichment in detritus-based soil animal communities; therefore, the analysis of variances in natural stable isotopes of nitrogen needs to be interpreted with caution. As results of the present study indicate, the postulated stepwise enrichment in $^{15}N$ by 3.4‰ per trophic level (Minagawa & Wada, 1984) is not universal, i.e. detritivores are likely to deviate from this rule. Results further indicate that the postulated $^{15}N$ discrimination in detritivores depends on nitrogen uptake, which in turn depends on the association of microorganisms with litter.

Overall, the results indicate that both species within trophic levels and species within taxonomic groups consist of trophic subguilds differing in food spectrum. Trophic differentiation is most pronounced in detritivores which comprise subguilds predominantly feeding on certain litter compartments, litter of different stages of decay and animal tissue. Taking them as trophic species or trophic levels, as commonly done in food web studies (Moore & De Ruiter, 1991; De Ruiter *et al*., 1996), therefore, is inappropriate. To develop strategies for improving the control of herbivore pest species by generalist predators, it is particularly important to identify predators which consume both decomposers and herbivores. Rather than ascribing species to fixed trophic levels, a more detailed delineation of trophically homogeneous groups is necessary for understanding food web links and interactions.

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## References

**Albers, D., Schaefer, M. & Scheu, S.** (2006) Incorporation of plant carbon into the soil animal food web of an arable system. *Ecology* **87**, 235–245.

**Bengtsson, J., Lundkvist, H., Saetre, P., Sohlenius, B. & Solbreck, B.** (1998) Effects of organic matter removal on the soil food web: forestry practices meet ecological theory. *Applied Soil Ecology* **9**, 137–143.

**Blower, J.G.** (1985) Millipedes. Synopses of the British Fauna (New Series) 35. London, Brill Backhuys.

**Briones, M.J.I., Ineson, P. & Sleep, D.** (1999) Use of $\delta^{13}C$ to determine food selection in collembolan species. *Soil Biology and Biochemistry* **31**, 937–940.

**Chahartaghi, M., Langel, R., Scheu, S. & Ruess, L.** (2005) Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biology and Biochemistry* **37**, 1718–1725.

**Chen, B., Snider, R.J. & Snider, R.M.** (1996) Food consumption by Collembola from northern Michigan deciduous forest. *Pedobiologia* **40**, 149–161.

**Chinery, M.** (1993) *Parey's Buch der Insekten*. Hamburg and Berlin, Germany, Verlag Paul Parey.

**Coleman, D.C. & Crossley, D.A.** (1996) Fundamentals of Soil Ecology. San Diego, California, USA, Academic Press.

**De Ruiter, P.C., Neutel, A.M. & Moore, J.C.** (1996) Energetics and stability in below-ground food webs. pp. 201–210 *in* Polis, G.A. & Winemiller, K.O. (*Eds*) *Food Webs. Integration of Patterns and Dynamics*. New York, USA, Chapman and Hall.

**Dücker, A., Schmüser, H., Heubel, K., Borcherding, R., Heubel, V., Müller-Reich, C., Pahnke, K., Gienapp, P., Nötzold, R. & Nötzold, V.** (1997) *Laufkäfer*. Hamburg, Germany, Deutscher Jugendbund für Naturbeobachtung.

**Dunger, W.** (1983) *Tiere im Boden. 3. Auflage. Neue Brehm-Bücherei*. A. Wittenberg Lutherstadt, Germany, Ziemsen-Verlag.

**Eisenbeis, G. & Wichard, W.** (1985) *Atlas zur Biologie der Bodenarthropoden*. Stuttgart, Germany, Gustav Fischer Verlag.

**Ernsting, G.** (1977) Aspects of predation and the coexistence of collembolan prey species. *Ecological Bulletins (Stockholm)* **25**, 478–480.

**Ernsting, G., Isaaks, J.A. & Berg, M.P.** (1992) Life cycle and food availability indices in Notiophilus biguttatus (Coleoptera, Carabidae). *Ecological Entomology* **17**, 33–42.

**Fisler, J.S., Drenick, E.J., Blumfeld, D.E. & Swendseid, M.E.** (1982) Nitrogen economy during very low calorie and very low protein diets. *American Journal of Clinical Nutrition* **35**, 471–486.

**Fjellberg, A.** (1980) *Identification keys to the Norwegian Collembola*. Ås, Norway, Norsk Entomologisk Forening.

**Freude, H., Harde, K.W. & Lohse, G.A.** (1976) *Die Käfer Mitteleuropas, Band 2 Adephaga 1*. Krefeld, Germany, Goecke & Evers.

**Gannes, L.Z., O'Brien, D.M. & Martinez del Rio, C.** (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* **78**, 1271–1276.

**Hairston, N.G. & Hairston, N.G.** (1993) Cause-effect relationships in energy flow trophic structure, and interspecific interactions. *The American Naturalist* **142**, 379–411.

**Halaj, J. & Wise, D.H.** (2002) Impact of detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* **83**, 3141–3151.

**Handley, L.L. & Scrimgeour, C.M.** (1997) Terrestrial plant ecology and 15-N natural abundance: the present limits to interpredation for uncultivated systems with original data from a Scottish old field. *Advances in Ecological Research* **27**, 139–212.

**Harde, K.W. & Severa, F.** (1998) *Der Kosmos-Käferführer*. Stuttgart, Germany, Franckh'sche Verlagsbuchhandlung.

**Heimer, S. & Nentwig, W.** (1991) *Spinnen Mitteleuropas*. Berlin, Germany, Paul Parey.

**Honomichl, K.** (1998) *Jacobs/Renner-Biologie und Ökologie der Insekten. 3.Auflage*. Stuttgart, Germany, Gustav Fischer.

**Hopkin, S.P. & Read, H.J.** (1992) *The Biology of Millipedes*. New York, USA, Oxford University Press.

**Hövemeyer, K.** (1999) Abundance patterns in terrestrial dipteran communities. *Pedobiologia* **43**, 28–43.

**Hunt, H.W., Coleman, D.C., Ingham, E.R., Inham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P. & Morley, C.R.** (1987) The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* **3**, 57–68.

**Jones, D.** (1990) *Der Kosmos-Spinnenführer. Mitteleuropäische Spinnen und Weberknechte*. Stuttgart, Germany, Kosmos-Franckh'sche Verlagsbuchhandlung.

**Locket, G.H. & Millidge, A.F.** (1951) *British Spiders*, Vol. I, II. London, UK, Ray Society.

**McNabb, D.M., Halaj, J. & Wise, D.H.** (2001) Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. *Pedobiologia* **45**, 289–297.

**Minagawa, M. & Wada, E.** (1984) Stepwise enrichment of $^{15}N$ along food chains: Further evidence and the relation between Delta $^{15}N$ and animal age. *Geochimica et Cosmochimica Acta* **48**, 1135–1140.

**Moore, J.C. & De Ruiter, P.C.** (1991) Temporal and spatial heterogeneity of trophic interactions within below-ground food webs. *Agriculture Ecosystems and Environment* **34**, 371–397.

**Nadelhoffer, K.J. & Fry, B.** (1988) Controls of nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Science Society of America Journal* **52**, 1633–1640.

**Neilson, R., Hamilton, D., Wishart, J., Marriotti, C.A., Boag, L., Handley, L.L., Scrimgeour, C.M., McNicol, J.W. & Robinson, D.** (1998) Stable isotope natural abundances of soil, plants and soil invertebrates in an upland pasture. *Soil Biology and Biochemistry* **30**, 1773–1782.

**Nyffeler, M., Sterlling, W.L. & Dean, D.A.** (1994) How spiders make a living. *Environmental Entomology* **23**, 1357–1367.

**Oelbermann, K., Langel, R. & Scheu, S.** (2008) Utilization of prey from the decomposer system by predators of grassland. *Oecologia* **155**, 605–617.

**Ostrom, P.H., Colunga-Garcia, M. & Gage, S.H.** (1997) Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence. *Oecologia* **109**, 108–113.

**Peterson, B.J. & Fry, B.** (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* **18**, 293–320.

**Pearson, S.F., Levey, D.J., Greenberg, C.H. & Martinez del Rio, C.** (2003) Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia* **135**, 516–523.

**Polis, G.A.** (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *The American Naturalist* **138**, 123–155.

**Polis, G.A. & Strong, D.R.** (1996) Food web complexity and community dynamics. *The American Naturalist* **147**, 813–846.

**Polis, G.A., Myers, C.A. & Holt, R.D.** (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Reviews of Ecology and Systematics* **20**, 297–330.

**Pollierer, M., Langel, R., Scheu, S. & Maraun, M.** (2009) Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). *Soil Biology and Biochemistry* **41**, 1221–1226.

**Ponsard, S. & Arditi, R.** (2000) What can stable isotopes (delta $^{15}N$ and delta $^{13}C$) tell about the food web of soil macroinvertebrates? *Ecology* **81**, 852–864.

**Post, D.M.** (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* **83**, 703–718.

**Reineking, A., Langel, R. & Schikowski, J.** (1993) $^{15}N$, $^{13}C$-online-measurements with an elemental analyser (Carlo Erba, NA 1500), a modified trapping box and a gas isotope mass spectrometer (Finnigan, MAT 251). *Isotopenpraxis Environmental Health Studies* **29**, 169–174.

**Roberts, M.J.** (1995) *Collins Field Guide. Spiders of Britain and Northern Europe*. London, UK, HarperCollins Publishers.

**Rusek, J.** (1998) Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation* **7**, 1207–1219.

**Sauer, F.** (1996) *Wanzen und Zikaden*. Karlsfeld, Germany, Fauna-Verlag.

**Sauer, F.** (1998) *Fliegen und Mücken*. Karlsfeld, Germany, Fauna-Verlag.

**Schaefer, M.** (1990) The soil fauna of a beech forest on limestone: trophic structure and energy budget. *Oecologia* **82**, 128–136.

**Schaefer, M.** (1991) The animal community: diversity and resources. pp. 51–120 *in* Röhrig, E. & Ulrich, B. (*Eds*) *Temperate Deciduous Forests. Ecosystems of the World*. Amsterdam, The Netherlands, Elsevier.

**Schaefer, M.** (1992) *Brohmer – Fauna von Deutschland*. Heidelberg, Germany, Quelle & Meyer.

**Scheu, S.** (2002) The soil food web: structure and perspectives. *European Journal of Soil Biology* **38**, 11–20.

**Scheu, S. & Falca, M.** (2000) The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia* **123**, 285–296.

**Scheu, S. & Setälä, H.** (2002) Multitrophic interactions in decomposer food webs. pp. 223–264 *in* Tscharntke, T. & Hawkins, B.A. (*Eds*) *Multitrophic Level Interactions*. Cambridge, UK, Cambridge University Press.

**Schimel, J.P. & Hättenschwiler, S.** (2007) Nitrogen transfer between decomposing leaves of different N status. *Soil Biology and Biochemistry* **39**, 1428–1436.

**Schmidt, O., Scrimgeour, C.M. & Handley, L.L.** (1997) Natural abundance of $^{15}N$ and $^{13}C$ in earthworms from a wheat and a wheat-clover field. *Soil Biology and Biochemistry* **29**, 1301–1308.

**Schmidt, O., Curry, J.P., Dyckmans, J., Rota, E. & Scrimgeour, C.M.** (2004) Dual stable isotope analysis (d13C and d15N) of soil invertebrates and their food sources. *Pedobiologia* **48**, 171–180.

**Steele, K.W. & Daniel, R.M.** (1978) Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of $^{15}N$ for tracer studies. *Journal of Agricultural Science* **90**, 7–9.

**Striganova, B.R.** (1967) Über die Zersetzung von überwinterter Laubstreu durch Tausendfüßer und Landasseln. *Pedobiologia* **7**, 125–138.

**Sunderland, K.D.** (1975) The diet of some predatory arthropods in cereal crops. *Journal of Applied Ecology* **12**, 507–515.

**Sunderland, K.D., Crook, N.E., Stacey, D.L. & Fuller, B.J.** (1987) A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology* **24**, 907–933.

**Swift, M.F., Heal, O.W. & Anderson, J.M.** (1979) *Decomposition in terrestrial ecosystems*. Berkeley, California, USA, University of California Press.

**Tayasu, I.** (1998) Use of carbon and nitrogen isotope ratios in termite research. *Ecological Research* **13**, 377–387.

**Tayasu, I., Abe, T., Eggleton, P. & Bignell, D.E.** (1997) Nitrogen and carbon isotope ratios in termites – an indicator of trophic habit along the gradient from wood-feeding to soil-feeding. *Ecological Entomology* **22**, 343–351.

**Vanderklift, M.A. & Ponsard, S.** (2003) Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. *Oecologia* **136**, 169–182.

**Verhoef, H.A., Prast, J.E. & Verweij, R.A.** (1988) Relative importance of fungi and algae in the diet and nitrogen nutrition of *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock) (Collembola). *Functional Ecology* **2**, 195–201.

**Wachmann, E., Platen, R. & Barndt, D.** (1995) *Laufkäfer: Beobachtung und Lebensweise*. Augsburg, Germany, Naturbuch-Verlag.

**Wallwork, J.A.** (1976) *The Distribution and Diversity of Soil Fauna*. London, UK, Academic Press.

**Wedin, D.A., Tieszen, L.L., Dewey, B. & Pastor, J.** (1995) Carbon isotope dynamics during grass decomposition and soil organic matter formation. *Ecology* **76**, 1383–1392.

**Werner, M.R. & Dindal, D.L.** (1987) Nutritional Ecology of soil arthropods. In: Nutritional ecology of insects, mites, spiders and related invertebrates. pp. 815–836 *in* Slansky, F. & Rodriguez, J.G. (*Eds*) *Nutritional Ecology of Insects, Mites, and Spiders*. New York, USA, J. Wiley.

**Witt, R.** (1998) *Wespen – beobachten, bestimmen*. Augsburg, Germany, Naturbuch-Verlag.

**Wolters, V.** (1985) Untersuchung zur Habitatbindung und Nahrungsbiologie der Springschwänze (Collembola) eines Laubwaldes unter besonderer Berücksichtigung ihrer Funktion in der Zersetzerkette. PhD dissertation, University of Göttingen, Göttingen, Germany.

**Yoneyama, T., Handley, L.L., Scrimgeour, C.M., Fisher, D.B. & Raven, J.A.** (1997) Variations of the natural abundances of nitrogen and carbon isotopes in Triticum aestivum, with special reference to phloem and xylem exudates. *New Phytologist* **137**, 205–213.

**Zachariae, G.** (1963) Was leisten Collembolen für den Waldhumus? pp. 109–124 *in* Doeksen, J. & van der Drift, J. (*Eds*). *Proceedings of the Colloquium on Soil Fauna, Soil Microflora and their Relationships*. Amsterdam, The Netherlands, North-Holland Publishing Company.

**Zahradnik, J.** (1985) *Käfer Mittel- und Nordwesteuropas*. Hamburg, Germany, Paul Parey.

**Zettel, J., Zettel, U., Suter, C., Streich, S. & Egger, B.** (2002) Winter feeding behaviour of Ceratophysella sigillata (Collembola: Hypogastruridae) and the significance of eversible vesicles for resource utilisation. *Pedobiologia* **46**, 404–413.

**Zheng, D.W., Bengtsson, J. & Agren, G.I.** (1997) Soil food webs and ecosystem processes-decomposition in donor-control and Lotka-Volterra systems. *American Naturalist* **149**, 125–148.

**Zimmermann, M. & Spence, J.R.** (1989) Prey use of the fishing spider Dolomedes triton (Pisauridae, Araneae): An important predator of the neuston community. *Oecologia* **80**, 187–194.

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## Appendix

Species composition of statistical homogeneous subgroups, their assignment to trophic subguilds (B, base of the food web; H1–H3, herbivores; D1–D7, detritivores; P1–P4, predators and N1–N3, necrovores), their $\delta^{15}N$ signatures (±SD) and main habitat.

| Trophic subguild | Taxa | $\delta^{15}N$ [‰] | main habitat |
|---|---|---|---|
| B | | −3.3±1.4 | |
| | Forest litter | −4.9±01 | |
| | Boundary litter | −2.7±1.0 | |
| | Meadow litter | −2.1±0.1 | |
| H1 | *Anoscopus albifrons* (Homoptera: Cicadellidae) | −4.3±0.2 | forest, meadow |
| H2 | *Muellerianella* sp. (Homoptera: Delphacidae) | −3.0±1.1 | boundary |
| H3 | *Jassargus pseudocellaris* (Homoptera: Cicadellidae) | −2.9±0.3 | meadow |
| D1 | *Orchesella flavescens* (Collembola: Entomobryidae) | −5.4±0.7 | forest |
| D2 | | −4.9±0.3 | |
| | *Tomocerus longicornis* (Collembola: Entomobryidae) | −4.7±0.5 | forest |
| | *Allajulus* sp. (Diplopoda: Julidae) | −5.1±1.3 | forest |
| D3 | *Glomeris* sp. adult (Diplopoda: Glomeridae) | −4.1±0.6 | boundary |
| D4 | Macrosternodesmidae (Diplopoda) | −3.1±0.6 | boundary |
| D5 | | −2.1±0.5 | |
| | *Glomeris* sp. juvenile (Diplopoda: Glomeridae) | −2.8±0.1 | boundary |
| | *Oniscus asellus* (Isopoda: Oniscidae) | −2.0±0.6 | boundary |
| | *Lepidocyrtus* sp. (Collembola: Entomobryidae) | −1.9±0.3 | meadow |
| | *Atomaria* sp. (Coleoptera: Cryptophagidae) | −1.7±0.9 | boundary |
| D6 | | −0.5±0.9 | |
| | *Porcellium conspersum* (Isopoda: Porcellionidae) | −0.8±0.4 | boundary |
| | *Ligidium hypnorum* (Isopoda: Ligiidae) | −1.6±1.8 | boundary |
| | *Cartodere* sp. (Coleoptera: Lathridiidae) | −0.9±1.0 | boundary |
| | Drosophilidae (Diptera) | 0.1±0.2 | boundary |
| | Sciaridae (Diptera) | 0.6±0.9 | forest |
| D7 | | 2.7±0.4 | |
| | Phoridae (Diptera) | 3.0±1.9 | forest |
| | Cecidomyiidae (Diptera) | 2.4±0.3 | boundary |
| P1 | *Notiophilus biguttatus* (Coleoptera: Carabidae) | −2.0±0.7 | boundary |
| P2 | | 0.7±1.1 | |
| | Carabid larvae (Coleoptera: Carabidae) | −1.4±0.2 | |
| | *Amara* sp. (Coleoptera: Carabidae) | −1.4±1.9 | meadow, boundary |
| | *Carabus nemoralis* (Coleoptera: Carabidae) | −0.7±0.5 | forest |
| | *Carabus intricatus* (Coleoptera: Carabidae) | −0.6±0.2 | meadow, boundary |
| | *Carabus coriaceus* (Coleoptera: Carabidae) | 0.1±0.6 | forest |
| | *Carabus glabratus* (Coleoptera: Carabidae) | 0.5±0.8 | forest |
| | *Leistus rufomarginatus* (Coleoptera: Carabidae) | −0.4±0.4 | forest |
| | *Abax parallelepipedus* (Coleoptera: Carabidae) | −0.03±0.4 | forest |
| | *Pterostichus oblongopunctatus* (Coleoptera: Carabidae) | 0.7±0.8 | forest, boundary |
| | *Harpalus latus* (Coleoptera: Carabidae) | 1.7±5.6 | – |
| | *Zora spinimana* (Araneae: Zoridae) | −1.3±0.6 | boundary |
| | *Euophrys frontalis* (Araneae: Salticidae) | −0.2±0.5 | forest |
| | *Oxyptila praticola* (Araneae: Thomisidae) | 0.1±0.8 | meadow, boundary |
| | *Histopona torpida* (Araneae: Agelenidae) | 0.7±0.6 | forest |
| | *Coelotes terrestris* (Araneae: Agelenidae) | 1.4±1.2 | forest |
| | *Pardosa lugubris* adult (Araneae: Lycosidae) | 0.7±0.8 | forest, boundary |
| | *Pardosa lugubris* juvenile (Araneae: Lycosidae) | 1.1±0.7 | forest, boundary |
| | *Pirata uliginosus* adult (Araneae: Lycosidae) | 1.7±1.4 | – |
| | *Trochosa terricola* adult (Araneae: Lycosidae) | 2.1±1.2 | boundary |
| | *Pardosa pullata* juvenile (Araneae: Lycosidae) | 2.1±0.7 | meadow |
| | *Pisaura mirabilis* (Araneae: Pisauridae) | 1.5±1.1 | boundary |
| | *Zelotes latreillei* (Araneae: Gnaphosidae) | 2.2±2.1 | meadow, boundary |
| | *Stenus* sp. (Coleoptera: Staphylinidae) | 1.4±0.7 | meadow, boundary |
| | *Ocypus* sp. (Coleoptera: Staphylinidae) | 1.5±1.0 | meadow, boundary |
| | *Othius punctatus* (Coleoptera: Staphylinidae) | 1.9±0.7 | meadow, boundary |
| | *Stilicus orbiculatus* (Coleoptera: Staphylinidae) | 2.2±0.4 | meadow, boundary |

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Appendix 1. Continued

| Trophic subguild | Taxa | $\delta^{15}N$ [‰] | main habitat |
|---|---|---|---|
| | *Ilyobates subopacus* (Coleoptera: Staphylinidae) | 2.2 ± 0.1 | meadow, boundary |
| | *Philonthus* sp. (Coleoptera: Staphylinidae) | 1.7 ± 1.9 | meadow, boundary |
| | *Neobisium* sp. (Pseudoscorpiones: Neobisiidae) | −0.5 ± 0.9 | forest, boundary |
| | *Stenichnus collaris* (Coleoptera: Scydmaenidae) | −0.3 ± 0.1 | boundary |
| | *Lithobius* sp. (Chilopoda: Lithobiidae) | 0.1 ± 1.0 | boundary |
| | *Nemastoma lugubre* (Opiliones: Nemastomatidae) | 0.4 ± 0.7 | boundary |
| | *Lopophilio palpinalis* (Opiliones: Phalangiidae) | 1.0 ± 0.7 | boundary |
| P3 | | 3.2 ± 0.3 | |
| | Asilidae (Diptera) | 3.2 ± 0.7 | boundary |
| | *Xysticus bifasciatus* (Araneae: Thomisidae) | 2.6 ± 0.9 | meadow |
| | *Tegenaria sylvestris* (Araneae: Agelenidae) | 2.6 ± 0.4 | forest, boundary |
| | *Pachygnatha degeeri* (Araneae: Tetragnathidae) | 3.1 ± 0.7 | meadow |
| | *Trochosa terricola* juvenile (Araneae: Lycosidae) | 3.2 ± 0.8 | boundary |
| | *Alopecosa pulverulenta* adult (Araneae: Lycosidae) | 3.3 ± 1.8 | meadow, boundary |
| | *Alopecosa pulverulenta* juvenile (Araneae: Lycosidae) | 3.2 ± 0.7 | meadow, boundary |
| | *Zelotes praeficus* (Araneae: Gnaphosidae) | 3.4 ± 0.9 | meadow, boundary |
| | *Erythraeus* sp. (Acari: Prostigmata: Erythraeidae) | 3.1 ± 0.3 | boundary |
| | *Dyschirius globosus* (Coleoptera: Carabidae) | 3.2 ± 0.6 | meadow |
| | *Poecilus* sp. (Coleoptera: Carabidae) | 3.5 ± 0.2 | meadow |
| | Staphylinid larvae (Coleoptera: Staphylinidae) | 3.2 ± 0.1 | meadow, boundary |
| | Dytiscidae (Coleoptera) | 3.5 ± 2.1 | meadow |
| P4 | | 3.8 ± 0.4 | |
| | *Pardosa pullata* adult (Araneae: Lycosidae) | 3.5 ± 0.6 | meadow |
| | *Dolomedes fimbriatus* (Araneae: Pisauridae) | 4.1 ± 0.6 | meadow |
| N1 | *Ptomaphagus* sp. (Coleoptera: Catopidae) | 5.4 ± 0.3 | boundary |
| N2 | *Necrophorus vespilloides* (Coleoptera: Silphidae) | 6.0 ± 1.0 | boundary |
| N3 | Sarcophagidae (Diptera) | 7.2 ± 1.9 | boundary |

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