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Feeding guilds in Collembola based on nitrogen stable isotope ratios

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Abstract

In soil a high number of species co-exist without extensive niche differentiation, which was assigned as 'the enigma of soil animal species diversity'. In particular, the detritivores are regarded as food generalists. We have investigated nitrogen stable isotope ratios ($^{15}N/^{14}N$) of a major decomposer group, the Collembola, to evaluate trophic relationship and determine feeding guilds. Additionally, the $\delta^{15}N$ values of potential food sources such as mosses, lichens and other plant derived material (bark, nuts, leaves) were analysed. The natural variation in nitrogen isotopes was assessed in 20 Collembola taxa from three deciduous forest stands. The $\delta^{15}N$ signature formed a continuum from phycophages/herbivores to primary and secondary decomposers, reflecting a gradual shift from more detrital to more microbial diets. The $\delta^{15}N$ gradient spanned over 9 δ units, which implies a wide range in food sources used. Assuming a shift in ^{15}N of about 3 ‰ per trophic level, the results indicate a range of three trophic levels. These variations in $^{15}N/^{14}N$ ratios suggest that trophic niches of Collembola species differ and this likely contributes to Collembola species diversity.

Keywords: Collembola; Nitrogen stable isotopes; $^{15}N/^{14}N$ ratios; Feeding guilds

1. Introduction

Collembola are among the most abundant soil-dwelling arthropods with densities up to several million individuals per square meter in forest soils (Petersen and Luxton, 1982). Worldwide about 7000 species are described, and species richness per site ranges from 3 to 60 depending on the ecosystem (Rusek, 1998). Although decomposition is mainly due to microbial activity, the soil fauna is an important driver of these processes by conditioning the litter and stimulating microbial activity. Collembola play an important role in plant litter decomposition and in forming soil microstructure (Visser, 1985; Klironomos and Kendrick, 1995; Rusek, 1998). They affect nutrient cycling through litter comminution, dissemination of microorganisms and grazing (Moore et al., 1987; Addison et al., 2003).

Generally, soil detritivores are regarded as food generalists with a low degree in nutritional specialisation (Scheu and Setälä, 2002). Studies on feeding strategies in Collembola concluded that the majority of euedaphic and hemiedaphic species feed unselectively on a wide variety of food materials (Hopkin, 1997). Depending on the resources available, they ingest bacteria, fungi, algae, plant litter, or other soil animals, such as protozoa, nematodes, rotifers, and enchytraeids (Parkinson, 1988; Rusek, 1998; Scheu, 2002). Several studies have demonstrated the importance of fungi in Collembolan nutrition (Visser et al., 1987; Chen et al., 1995; Klironomos and Kendrick, 1995). However, other studies documented preferences for certain types of fungi in some species of Collembola (Visser and Whittaker, 1977; Hiol et al., 1994; Thimm and Larink, 1995; Sadaka-Laulan et al., 1998). Additionally, Lee and Widden (1996) showed that species such as *Folsomia candida,* which commonly are assumed to consume fungi, preferentially feed on nematodes when offered a choice. Overall, this suggests that trophic relationships are unspecific with a broad overlap in resources and that to ascribe Collembola species to trophic levels or feeding guilds is difficult.

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Collembola diets are usually verified by analysis of gut contents or by observations of feeding behaviour in laboratory experiments. Due to this the assigned feeding guilds often reflect more taxonomic rather than functional relationships. Besides, feeding preferences found in the laboratory are difficult to prove under field conditions. Over the last decade nitrogen stable isotope analysis has been used as powerful tool in food web studies (Gannes et al., 1997, 1998; Ponsard and Arditi, 2000). Isotopic ratios of $^{15}N/^{14}N$ were applied to ascribe animals to trophic levels, as the $^{15}N/^{14}N$ ratios of consumers exceed those of their diets. Within food chains this results in a stepwise enrichment of the heavier nitrogen isotope of about 3‰ per trophic level (Minagawa and Wada, 1984; Wada et al., 1991; Eggers and Jones, 2000, Post, 2002). Furthermore, in contrast to gut content analyses and food choice experiments, nitrogen stable isotope ratios reflect the long-term trophic relationship of animals (Scheu and Falca, 2000). In sum this technique allows in situ investigation of diet history within a broader window of time.

In this study we determined the $^{15}N/^{14}N$ signatures in Collembola collected from three different deciduous forest sites. The aim of the study was to analyse if (i) various species in a community differ in their stable isotope ratio indicating separate feeding strategies (ii) different niches with respect to food resource are irrespective of forest type, and (iii) species can be classified in consistent feeding guilds according to stable isotope ratios.

2. Materials and methods

2.1. Study sites

The Collembola were obtained from litter samples of three forest stands, the Kranichsteiner Wald (K), the Göttinger Wald (G) and the Solling (S). The Kranichsteiner Wald is an oak-beech forest located 8 km northeast of Darmstadt, South Germany, at 150–175 m a.s.l. Parent rock is rothliegendes covered with sand. The soil types are dystric gleysols and orthic luvisols (FAO-UNESCO classification); the humus form is moder. The pH of the soil varies between 3.6 and 4.3. The tree layer is dominated by oak (*Quercus robur*), about 190 years old, with interspersed beech (*Fagus sylvatica*). The understory is dominated by hornbeam (*Carpinus betulus*), about 125 years old. The herb layer is dominated by *Luzula luzuloides*, *Milium effusum*, *Anemone nemorosa*, *Oxalis acetosella*, *Deschampsia cespitosa*, *Stellaria holostea*, *Melampyrum pratense* and *Polytrichum formosum*.

The Göttinger Wald is a 130 years old beech forest (*F. sylvatica*) located on a limestone plateau east of Göttingen (Lower Saxony, Germany) at 420 m a.s.l. The soil is an orthic rendzina type with mull humus. The soil pH ranges from 4.4 to 7.0 with an average of 5.3. Among the beech, maple (*Acer platanoides* and *A. pseudoplatanus*) and ash trees (*Fraxinus excelsior*) are interspersed. The species rich herb layer is dominated by *Allium ursinum*, *Mercurialis perennis* and *Anemone nemorosa*.

The Solling is a mature beech stand about 135 years old, located 50 km northwest of Göttingen on a mountain range at 500 m a.s.l. Parent rock is sandstone covered with a loess layer of about 1 m. The soil type is a dystric cambisol, the humus form is moder. The soil pH ranges between 3.3 and 4.4. The understory is formed mainly by small patches of *Luzulua luzuloides*.

2.2. Sampling

The sampling was carried out in all three forest stands in the L/F layer in October 2003. Collembola were extracted by heat at 45 °C for two days with a Kempson Extractor (Kempson et al., 1963). Animals were collected in water and separated under a dissecting microscope. Collembola were determined to species or higher taxonomic level, and stored in a concentrated NaCl solution until analysis.

For measurement of nitrogen isotope ratios and total N content the specimens were transferred into tin capsules and dried at 60 °C for 48 h. Samples were weighed and stored in a desiccator. Generally three replicates were analysed, whereby each sample consisted of pooled individuals (between 1 and 120 specimens based on body size of the species) to obtain sufficient material for ^{15}N analysis.

Samples of potential food sources for Collembola were taken in the forest stand in Kranichstein. Algae, lichens and different materials originating from trees (bark, branches, rooting wood, nuts, leaves) were collected, dried at 60 °C for 72 h, and ground by a blender. Three replicates each were analysed for nitrogen stable isotopes.

2.3. ^{15}N analysis

The $^{15}N/^{14}N$ ratios and total N content of samples were determined by a coupled system of an elemental analyser (NA 1500, Carlo Erba, Milan) and a mass spectrometer (MAT 251, Finnigan). Stable isotope abundance is expressed using the δ notation with $\delta^{15}N$ (‰) $= (R_{sample} - R_{standard})/R_{standard} \times 1000$. R_{sample} and $R_{standard}$ represent the $^{15}N/^{14}N$ ratios of the sample and standard, respectively. Atmospheric nitrogen served as the primary standard and acetanilide (C_8H_9NO, Merck, Darmstadt) for internal calibration.

2.4. Statistical analysis

Data on body weight, N content and $\delta^{15}N$ were subjected to correlation analysis using Pearson's correlation coefficient. Additionally, $\delta^{15}N$ in Collembolan species was analysed using ANOVA. If significant differences were found, pairs of treatments were compared by Tukey's HSD test. Statistical analyses were performed using JMP 3.1 for Macintosh (SAS Institute Inc., Cary, USA).