Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms[☆]

Anton A. Potapov [a, *], Eugenia E. Semenina [a], Anastasiya Yu. Korotkevich [b], Natalia A. Kuznetsova [b], Alexei V. Tiunov [a]

[a] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, Moscow 119071, Russia
[b] Moscow State Pedagogical University, Kibalchicha str. 6, Moscow 129164, Russia

ARTICLE INFO

ABSTRACT

Collembola are among the most abundant, diverse and functionally important groups of soil animals. Collembolans inhabit different litter and soil layers and their food objects are intimately related to their habitat. Morphological differences that separate high rank taxa of collembolans have clear functional meaning in relation to life style and habitat requirements (including position in the soil profile). However, no study has tested the hypothesis that the species within the major functional groups also differ in terms of trophic positions. This hypothesis was tested for the first time using stable isotope analysis. We compiled original and published data on the stable isotope composition of 82 collembolan species in temperate forest ecosystems. The $\delta^{13}C$ and $\delta^{15}N$ values of collembolans were found related to their life forms, reflecting a shift in available food objects across different habitat layers and matching the vertical isotopic gradient of soil organic matter. The trophic niche of species varied among different collembolan orders and families, indicating a pronounced phylogenetic signal and supporting the trophic niche conservatism hypothesis. Considering stable isotope compositions, as well as the taxonomic identity and life form of species, we outlined four collembolan functional guilds that use different types of food and perform different ecosystem functions.

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1. Introduction

Relating the taxonomic structure to the functioning of soil communities remains a challenging task in soil ecology. The majority of reconstructions of soil food web structure operate with taxonomic units as a proxy of functional groups (e.g. Berg and Bengtsson, 2007; De Ruiter et al., 1996). This assumption silently follows the evolutionary 'niche conservatism' principle, which implies that closely related species have similar fundamental ecological niches due to shared inherited traits (Losos, 2008; Peterson et al., 1999; Wiens and Graham, 2005). The segregation of ecosystem functions is well seen among kingdoms of life and becomes less clear at the lower levels of taxonomic resolution. The use of higher taxonomic units instead of species (so-called 'taxonomic sufficiency') is widely discussed in applied ecology (Ellis, 1985; Terlizzi et al., 2003). The sufficiency of taxonomic units while reconstructing the soil food web structure depends on the aims of a particular study, and might vary in different animal lineages (Bhusal et al., 2014; Caruso and Migliorini, 2006; Groc et al., 2010).

Collembola are among the most abundant groups of soil decomposers, inhabiting various organic substrates and using a wide range of food sources (Christiansen, 1964; Rusek, 1998). Collembolans affect ecosystem functioning by regulating the soil microbial activity by direct feeding on microorganisms, as well as by changing the soil structure through litter comminution, casting and other mechanisms (Faber and Verhoef, 1991; Maaß et al., 2015; McGonigle, 1995). There is a pronounced variation in trophic specialization among collembolans (Chahartaghi et al., 2005; Ferlian et al., 2015; Pollierer et al., 2009) that can be ascribed to high heterogeneity of the environment. Indeed, food objects of collembolans are strongly related to their habitat. For instance, in the upper litter layers collembolans may consume micro-algae, whereas in lower litter strata they rely on detritus and fungal mycelium (Ponge, 2000). Because of this, collembolan species of

the different life forms (*sensu* Gisin, 1943) that inhabit different litter layers or soil depths are expected to differ in their trophic niches. On the other hand, the range of the habitats and food sources that can be used by a species is constrained by evolutionarily inherited morphological traits shared within high-rank taxonomic groups. The taxonomic identity and habitat layer are therefore expected to shape the trophic niches of collembolan species, but this notion has not been explicitly tested.

Stable isotope analysis (SIA), an increasingly widespread technique, provides a powerful tool to quantitatively estimate the parameters of trophic niches (Layman et al., 2007). Generally, the $\delta^{15}N$ values (reflecting $^{15}N/^{14}N$ ratio) indicate the trophic level of an animal while $\delta^{13}C$ values ($^{13}C/^{12}C$ ratio) often differ depending on basal food sources (Post, 2002; Tiunov, 2007). Among the main food sources of collembolans, algae and other primary producers (lichens, some mosses) obtaining nitrogen mainly from atmospheric deposits are depleted in ^{15}N relative to other plants (Delgado et al., 2013; Solga et al., 2005). Mycelium of ectomycorrhizal fungi is enriched in ^{15}N, whereas saprotrophic microorganisms are enriched in ^{13}C relative to plant litter (Taylor et al., 2003; Wallander et al., 2004; Tiunov et al., 2015). Finally, the ^{13}C and ^{15}N contents increase with soil depth (Garten et al., 2000; Ponsard and Arditi, 2000). Thus, the range of food items and energy fluxes (e.g. saprotrophic/mycorrhizal) utilized by different collembolans can be estimated using $\delta^{15}N$ and $\delta^{13}C$ values (Potapov and Tiunov, 2016). In spite of the increasing accumulation of data on the isotopic composition of soil animals in various ecosystems, the structure of isotopic trophic niches has not been related to the taxonomic structure of soil organisms.

In this study, we compiled data, both original and published, on the isotopic composition of 82 collembolan species from temperate forest ecosystems, in order to analyze relationships between the trophic niches occupied, the taxonomic identity and life form identities of collembolan species. Based on this analysis, we discuss the ecological function of collembolans belonging to different trophic groups and occupying different layers of the soil and litter.

2. Material and methods

2.1. Data collection and compilation

2.1.1. Original data

We analyzed the stable isotope composition of 57 collembolan species from 12 families collected on 23 forest sites in five geographical locations in Russia (in toto, 973 samples, amounting to 200 species-forest site combinations, Supplementary Table S1). Forest types included spruce and pine-dominated stands, as well as mixed and deciduous forests. Collembolans were collected by extracting litter and mineral soil (up to a depth of 5 cm) samples using Tullgren funnels and identified according to Fjellberg (1998, 2007). After the identification animals were dried at 50 °C for at least 48 h.

Stable isotope analysis of collembolans and leaf litter (3–8 mixed samples of litter of dominating tree species per forest site) was conducted using a Thermo Delta V Plus continuous-flow IRMS coupled with an elemental analyzer located at the Institute of Ecology and Evolution, Moscow. The isotopic composition of N and C was expressed in the conventional δ-notation relative to international standards (atmospheric N_2 and VPDB, respectively). Samples were analyzed with reference gas (N_2 and CO_2) calibrated against IAEA reference materials (USGS 40, USGS 41 and IAEA-CH3). The drift was corrected using internal laboratory standards (casein and acetanilide). The standard deviation of $\delta^{15}N$ and $\delta^{13}C$ values of reference materials (n = 6–8) was <0.15‰.

2.1.2. Published data

Published data on the stable isotope composition of collembolans in temperate forest communities were searched using keywords "stable isotope" and "Collembola" in Google Scholar (https://scholar.google.com). Overall, seven articles were retrieved reporting data on 51 collembolan species from 8 families collected on 11 forest sites in Europe (Germany, Switzerland and Romania) and Japan (in toto, 89 species-forest site combinations; Supplementary Table S2).

2.1.3. Data compilation

Assuming that the general structure of soil animal food webs, as reflected in the stable isotope signatures, varies little with forest type (Klarner et al., 2014; Korobushkin et al., 2014, see also Fig. 3), we bulked published and original data from different forest sites and locations using litter-normalized δ values (see statistical analysis). Collembolan species were classified into higher rank taxa (families and orders) using a conservative system (Fjellberg, 2007, 1998), which is largely supported by more recent classifications (Deharveng, 2004) and phylogenetic analysis (Xiong et al., 2008). Species of the neustonic or corticicolous life form were excluded from the dataset due to low numbers of replications. In addition, one sample of *Ceratophysella sylvatica* and one sample of *Thaumanura caroli* were excluded as outliers. The resulting "total dataset" contained 82 collembolan species. In this dataset, $\delta^{15}N$ values only were reported for seven species and $\delta^{13}C$ values only − for two species (Table 1). After the exclusion of families represented by a single species (Neelidae, Odontellidae, and Arrhopalitidae), a shortened "bi-isotopic dataset" contained 70 species with both $\delta^{13}C$ and $\delta^{15}N$ values reported. Despite the limited number of species, we believe that our dataset is sufficiently representative, since it was compiled non-selectively and includes the majority of common collembolan species from temperate forest ecosystems.

2.2. Life forms

To reveal the trophic niches in relation to life forms (*sensu* Gisin, 1943) of collembolan species, we used a classification that included four life forms (Fig. 1; Table 1):

1. *Atmobiotic* life form: it corresponds to "atmobiotic macrophyte inhabitants" in Stebaeva (1970) or macro- and microphytobionts in Rusek (2007). These collembolans mostly inhabit macrophytes such as grasses, bushes, trunks and branches of trees, but still can be found on the litter surface. Atmobiotic species are large (up to 8–10 mm in length), brightly and often motley colored. They have long limbs and full set of ocelli; body shape can be either round or elongated.
2. *Epedaphic* life form: it corresponds to "upper-litter dwellers" of Stebaeva (1970) or epigeonts in Rusek (2007), inhabiting the upper litter layer or the surface of fallen logs. These collembolans are of medium or large size, with pronounced but frequently uniform coloring, in most cases with 6 + 6 or 8 + 8 ocelli. Limbs usually are less developed than in atmobiotic species.
3. *Hemiedaphic* life form: it corresponds to the "hemiedaphic" group of Stebaeva (1970) or to hemiedaphobionts in Rusek (2007), inhabiting partly decomposed litter or rotten wood. These collembolans are of medium or small size (ca. 1–2 mm), usually with dispersed pigmentation, reduced number of ocelli and shortened limbs.
4. *Euedaphic* life form: it corresponds to the "euedaphic" group of Stebaeva (1970) or to euedaphobionts in Rusek (2007), largely inhabiting the upper mineral layers of the soil (humus horizon). These collembolans tend to have elongated soft body of medium