Oecologia
https://doi.org/10.1007/s00442-024-05595-y

ORIGINAL RESEARCH

Incorporation of the ^{15}N-labeled simulated arthropod rain in the soil food web

Oksana L. Rozanova[1] · **Sergey M. Tsurikov**[1] · **Alexey A. Kudrin**[2] · **Vladislav D. Leonov**[1] · **Marina G. Krivosheina**[1] · **Dmitry N. Fedorenko**[1] · **Andrei V. Tanasevitch**[1] · **Leonid B. Rybalov**[1] · **Alexei V. Tiunov**[1]

Received: 16 April 2024 / Accepted: 8 July 2024

Abstract

Direct trophic links between aboveground and belowground animal communities are rarely considered in food web models. Most invertebrate animals inhabiting aboveground space eventually become prey of soil predators and scavengers forming a gravity-driven spatial subsidy to detrital food webs, but its importance remains unquantified. We used laboratory-grown ^{15}N-labeled Collembola to trace the incorporation of arthropod rain into soil food webs. Live or euthanized Collembola were supplemented once to field mesocosms in the amount equivalent to the mean daily input of the arthropod rain (19 mg d.w. m^{-2}). After the addition of live Collembola, the isotopic label was found most often in predatory Trombidiformes (83% of samples) and Mesostigmata mites (85%), followed by Araneae (58%), Chilopoda (45%), and Coleoptera (29%). Among non-predatory groups, the isotopic label was recorded in Thysanoptera (27%), Collembola (24%), and Oribatida (18%). The ^{15}N-label was also detected in Symphyla, Formicidae, Diplura, Diplopoda, Opiliones, Diptera, Hemiptera, Oligochaeta, and Nematoda. There was a positive correlation between natural ^{15}N abundance and the frequency of the isotopic label among predators, but not among decomposers. In the non-replicated treatment, in which dead collembolans were added, the label was found in predators and decomposers in approximately equal proportions (21–25%). Unlike other forms of the aboveground subsidy (such as leaf litter, frass, or honeydew) that are primarily processed by microorganisms, arthropod rain is assimilated directly by the animals. The high frequency of consumption of the aboveground subsidy suggests that it plays a significant role in maintaining the abundance of soil predators.

Keywords Aboveground-belowground linkage · Detrital food webs · Forest ecosystems · Isotopic label · *Folsomia candida*

Introduction

Interactions between above- and below-ground animal communities have important implications for ecosystem functioning (Van der Putten et al. 2009). Soil detrital food webs (based on dead organic matter) and aboveground grazing food webs (based on green plants) make up an inextricable functional unity (Wardle 2004). However, direct trophic links between aboveground and belowground communities are rarely considered in food web models (Jochum and Eisenhauer 2022). Interactions between aboveground and belowground biota are usually regarded through the prism of plant-mediated interactions or the activity of aboveground generalist predators that can receive a detrital subsidy from the soil (Bardgett et al. 1998; Scheu 2001; Halaj and Wise 2002). Direct links between belowground and aboveground food webs are, however, much more diverse and include many types of feedbacks, such as emerging insects with soil-associated larvae (Wallwork 1970), feeding of specialized aboveground predators on soil animals (Macdonald 1983; Martay and Pearce-Higgins 2020), consumption of honeydew and frass produced by herbivores (Seeger and Filser 2008; Milcu et al. 2015; Ritzenthaler et al. 2018), and also the flux of animals inhabiting aboveground space that fall on

---

Communicated by Liliane Ruess.

Alexei V. Tiunov
a_tiunov@mail.ru

[1] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, 119071 Moscow, Russia

[2] Institute of Biology of Komi Scientific Centre, Ural Branch of the Russian Academy of Sciences, Kommunisticheskaja 28, 167000 Syktyvkar, Russia

the soil surface, forming the so-called arthropod rain (Chan et al. 2008; Rozanova et al. 2019).

The multidimensional structure of the forest canopy and the variety of available resources (including those produced by epiphytes) support a great diversity and density of invertebrates (Müller et al. 2018) that eventually become prey of soil predators and scavengers forming a gravity-driven spatial subsidy to soil food webs (Pringle and Fox-Dobbs 2008). While this input of energy and nutrients (Schowalter and Crossley 1983) has been shown to play a crucial role in maintaining fish populations in small forest creeks (Kawaguchi and Nakano 2001; Baxter et al. 2005), its importance for the soil food webs has yet to be quantified.

The contribution of the arthropod rain in the diet of soil predators was suggested in several recent studies but received only indirect experimental support (Potapov et al. 2016; Goncharov et al. 2016), although allochthonous subsidy of soil predators is likely a widespread phenomenon (Polis and Strong 1996; Hodkinson et al. 2002). Our previous studies have shown the potential importance of arthropod rain in the functioning of forest ecosystems. In a mixed-temperate forest, the flux of invertebrates from the tree crowns to the soil in the summer averaged 19 mg d.w. m^2 day^{-1} (Rozanova et al. 2019), with about one-third consisting of dead animals and their derivatives. The arthropod rain is composed of animals dwelling in the tree crowns (mainly wingless invertebrates and larvae of insects), but also of winged animals partly originating from the soil (Rozanova et al. 2022).

To trace the assimilation pathways of the aboveground subsidy into detrital food webs, we used isotopic labeling of the simulated arthropod rain in a field experiment. Studies using isotope enrichment have long shown their convenience and effectiveness in a wide range of environmental experiments (Hood-Nowotny and Knols 2007). Collembola makes up a significant proportion of the arthropod rain in the studied forest, about 10% of the total biomass (Rozanova et al. 2019), thus the simulated arthropod rain was represented by ^{15}N-labeled *Folsomia candida* grown in laboratory conditions.

Thus, the purpose of this work was to determine the pathways and intensity of the incorporation of the animals falling from tree crowns in the soil detrital food web using an isotope-labeled analogue of the arthropod rain. We expected, that according to the "size channels hypothesis" (Potapov et al. 2021; Potapov 2022), Collembola will be consumed mainly by mesofauna, rather than macrofauna. Furthermore, we assumed that living and nonliving subsidies would be consumed at different rates by distinct trophic groups of soil fauna. We hypothesized that (1) Collembola, administrated at the daily amount typical of the arthropod rain flux, will be quickly consumed by various soil invertebrates, especially mesofauna, thus confirming that the arthropod rain subsidizes detrital food webs; (2) the consumption of the living Collembola should be more intense and/or frequent in predatory animals compared to saprophagous animals, whereas decomposers will actively consume dead collembolans.

Methods

Study site and experimental design

The experiment was conducted near Malinky Biological Station (Moscow region, Russia, 55°27′41″ N, 37°10′29″ E) in a mixed forest with spruce (*Picea abies* L.) and lime (*Tilia cordata* Mill.) forming the upper canopy. The soil is sandy loam sod podzolic (Folic Retisol Loamic, according to IUSS WRB 2014); ground vegetation is sparce and represented mainly by *Lamium galeobdolon, Asarum europaeum,* and *Pyrola minor*. Three experimental blocks were established in June, located at a distance of at least 20 m from each other (Supplementary Fig. S1). Each block included two or three 1 m^2 experimental plots subjected to different treatments, separated by a distance of 3–4 m. The plots were fenced with transparent polyethylene film on a light frame extending 5 cm below and 30 cm above the ground and covered with a mesh cloth (2 × 2 mm mesh size). Four pitfall traps were installed in the corners of each fenced plot. The traps were covered with lids, which were removed during sampling events.

At the beginning of the experiment, 19 mg d.w. (about 1200 specimens of different sizes) of alive ^{15}N-labeled springtails *Folsomia candida* Willem 1902 were added in one plot in each block (+ Coll treatment) while the second plot served as the control. Collembolans were evenly distributed over the soil surface. The amount of collembolans added was equivalent to the mean daily input of arthropods in the arthropod rain (19 mg dry weight m^{-2} day^{-1}; Rozanova et al. 2019). The dry mass of collembolans was estimated in a series of measurements of individuals of different ages. In addition, one experimental plot was established, in which frost-euthanatized ^{15}N-labeled *F. candida* were added in the same quantity (+ dColl treatment). This treatment was not replicated due to insufficient amounts of labeled collembolans. Thus, the experiment included three control plots without the addition of Collembola, three plots with the addition of living collembolans (+ Coll), and one plot with the addition of dead collembolans (+ dColl).

The ^{15}N-labeled collembolans were obtained from a laboratory culture, in which *F. candida* was kept in plastic containers on the peat substrate at room temperature and fed with an artificial food mixture containing ^{15}N ammonium chloride over 30 days. To prepare the food mixture, 10 g pectin, 5 g glucose, and 0.2 g ammonium chloride (98 at.% ^{15}N, Merck, Germany) were dissolved in 200 ml of distilled water and autoclaved. After cooling, the mixture was stored at 5 °C. Collembola were fed with the labeled mixture twice a week. The mixture was seemingly palatable and nutritious, as the number of collembolans increased during the incubation. The isotopic labeling of collembolans was successful, with mean δ^{15}N values of 6730‰ (SE 788, $n = 7$).

One day before the start of the experiment, collembolans intended to be used in the + Coll treatment plots were collected and kept on moistened filter paper until the release. Collembola used in the + dColl treatment were extracted from the remaining peat substrate using Tullgren funnels, and subsequently frozen at − 18 °C.

Soil fauna

Sampling of the soil fauna was carried out on days 8 and 22 after the addition of labeled collembolans. Aboveground macrofauna were caught manually and using pitfall traps. The traps were filled with water and left open for 24 h. Mesofauna were extracted from the 100 cm^2, 5 cm deep soil samples using Tullgren funnels. Three soil samples for the mesofauna extraction were taken from each experimental plot at each sampling event. Nematodes were extracted on Baermann funnels from the 19.6 cm^2, 5 cm deep soil samples, using three samples per plot. As we tried to minimize soil disturbance during intermediate sampling, earthworms were collected during the destructive sampling only on day 22. Large invertebrates were hand-sorted from the 25 × 25, 25 cm deep soil samples. The sampled animals were preserved in 75% ethanol and subjected to isotopic analysis after taxonomical identification.

Based on the taxonomic identity, morphological and behavioral traits, and isotopic studies (Striganova 1980; Potapov et al. 2022), all collected animals were attributed to five trophic groups: predators, decomposers, herbivores, parasitoids, and other/mixed feeders. All these groups were represented by at least three families. Parasitoids were sparce and represented by Hymenoptera and Diptera (Bombyliidae, Pipunculidae, Tachinidae). Decomposers included 15 families of Oribatida, Collembola (Isotomidae, Tomoceridae, Entomobryidae, Symphypleona), Diplopoda, Symphyla, imagoes and larvae of Coleoptera (Corylophidae, Cryptophagidae, Lathridiidae, Leiodidae, Ptiliidae), Diptera (Sphaeroceridae, Tipulidae, some Cecidomyiidae and Sciaridae), Oligochaeta (Enchytraeidae and Lumbricidae), and Nematoda (Plectidae). Predators were represented mainly by Araneae (Linyphiidae, Liocranidae, Lycosidae, Theridiidae, Thomisidae), Opiliones (Nemastomatidae, Phalangiidae), Chilopoda (Geophilidae and Lithobiidae), Coleoptera (Cantharidae, Carabidae, Staphylinidae), Diptera (Dolichopodidae, Empididae, Rhagionidae), Hymenoptera (Formicidae), Neuroptera, Mesostigmata (Gamasina, Uropodina), Trombidiformes, and Nematoda (Mononchidae). Herbivores were not numerous and included Hemiptera (Coccoidea, Aphidoidea, some Heteroptera), Thysanoptera, larval Coleoptera (Curculionidae, Nitidulidae, Scarabaeidae) and Diptera (some Cecidomyiidae), and Gastropoda. The group of other/mixed feeders included taxa with mixed or undefined feeding, e.g. larvae of Coleoptera (Elateridae), Diptera (Ceratopogonidae, some Sciaridae), Diplura, and Nematoda (Qudsianematidae).

Furthermore, we divided all invertebrates into two conventional size classes, i.e. meso- and macrofauna (Gongalsky 2021). As the number of analyzed samples of nematodes was small, they were excluded from this analysis.

Stable isotope analysis

All materials were dried at 50 °C for at least 72 h. For the isotope analysis, an aliquot of the homogenized individual (earthworms) or the abdomen of large arthropods was used. Smaller animals (d.w. less than 500 µg) were analyzed individually, while the smallest ones (less than 50 µg) were analyzed in a group of several individuals of the same taxonomic group. Mixed samples of the plant litter were ground to the powder using an MM200 ball mill (Retsch, Germany). Stable isotope analysis was performed using a Thermo Flash 1112 Elemental Analyzer and a Thermo Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, USA) in the Joint Usage Center “Instrumental Methods in Ecology” at the A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow.

The nitrogen isotopic composition was measured as deviations from the international standards (atmospheric N_2) and expressed in conventional δ values (‰): $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] * 1000$, where R_{sample} is the $^{15}N/^{14}N$ ratio in the sample and $R_{standard}$ is the $^{15}N/^{14}N$ ratio in the air N_2. The δ^{13}C values were measured relative to vPDB. An internal laboratory standard (protein B2155) was run every ten samples. The standard deviation of the δ^{15}N and δ^{13}C values in the laboratory standard was less than 0.15‰.

Data analysis

The natural stable isotope composition of non-labeled arthropods in the control treatment as well as of the litter collected on experimental plots before the experiment did not differ among the three blocks. Therefore, we did not use any data normalization or correction. Mean δ^{13}C and δ^{15}N values of the litter collected before the addition of the labeled collembolans were − 28.8 ± 0.2 and − 0.7 ± 0.1 ‰, respectively ($n = 20$, Supplementary Table S1).

The δ^{15}N values of soil animals vary in relatively wide limits due to their trophic position and other reasons (Potapov et al. 2019b, Supplementary Table S1).

Therefore, animals (or groups of animals combined in one sample) were assumed to be "labeled", i.e. to have consumed the ^{15}N-enriched collembolans or their derivatives, if their δ^{15}N values exceeded a certain threshold, which was set individually for each taxonomic group. For individual animals, the threshold was set as Q3 + 1.5*IQR of the δ^{15}N values of the corresponding taxon in the control treatment (family or genus, but occasionally order if the family has not been collected in the control treatment). For combined samples, the threshold was set as the maximum δ^{15}N value of the corresponding taxonomic group (family or genus) in the control treatment + 1‰.

Two main parameters were used to describe the occurrence and intensity of the label: (1) median δ^{15}N values of labeled samples, hereafter denoted as $\delta^{15}N_L$ (median [min–max], ‰), and (2) the proportion of labeled samples P_L of the total number of samples of a certain trophic or taxonomic group collected in experimental plots after labeling (mean value ± 1 SE, %, $n = 3$). To facilitate comparisons with other studies, central tendencies of natural δ^{13}C and δ^{15}N values were presented as means ± 1 SE.

Results (+ Coll treatment only) were analyzed using a series of one-way non-parametric Kruskal–Wallis analyses of variance with factors 'Trophic Group' (Decomposers, Predators, Herbivores, Others / mixed feeders, and Parasitoids), and 'Time' (day 8, day 22). Pairwise comparisons between macro- and mesofauna groups were performed using the Mann–Whitney *U* test. $P < 0.05$ was considered statistically significant. The relationships between natural δ^{15}N signatures of animal taxa and the proportion of labeled samples were assessed using Pearson correlation. Considering the trophic consistency of supraspecific taxa of soil animals (Potapov et al. 2019a), this analysis was performed at the family level. The calculations were performed using STATISTICA 10 (StatSoft, Tulsa, USA) and R 4.2.1 (R Core Team 2022) packages.

Results

δ^{15}N values and the proportion of labeled samples in soil consumers

Among five trophic groups, decomposers and predators were the most abundant, whereas parasitoids were collected only occasionally, although all trophic groups were present in all treatments. Isotope analysis was carried out for 1251 macro- and mesofauna samples, of which 444, 582, and 225 were obtained from the control, + Coll, and + dColl treatments, respectively. The natural (before labeling) δ^{15}N values of animals ranged from − 4.3 to 11.1‰ (Table S1). After the labeling, the maximum δ^{15}N values of the animals from the + Coll and + dColl treatments reached 628.6‰ and 194.5‰, respectively.

In the + Coll treatment, the proportion of labeled samples (P_L) depended strongly on the trophic group ($H = 15.9$, $P = 0.003$). The isotopic label was received mainly by predators (nearly 55.6% of the samples) which were followed by mixed feeders (25.6%) and decomposers (16.3%) (Fig. 1, Table S2). In the non-replicated + dColl treatment, the label was found in predators and decomposers in approximately equal proportions (21–25%).

The proportion of labeled samples did not depend significantly on the time of sampling, but on day 8 mean P_L value across all treatments and trophic groups was higher (29.3 ± 1.9%) than on day 22 (21.28 ± 1.0%).

Among predators and decomposers in the + Coll treatment, mesofauna ($P_L = 82.5$ and 18.5%, respectively) received the label more often than macrofauna ($P_L = 44.3$

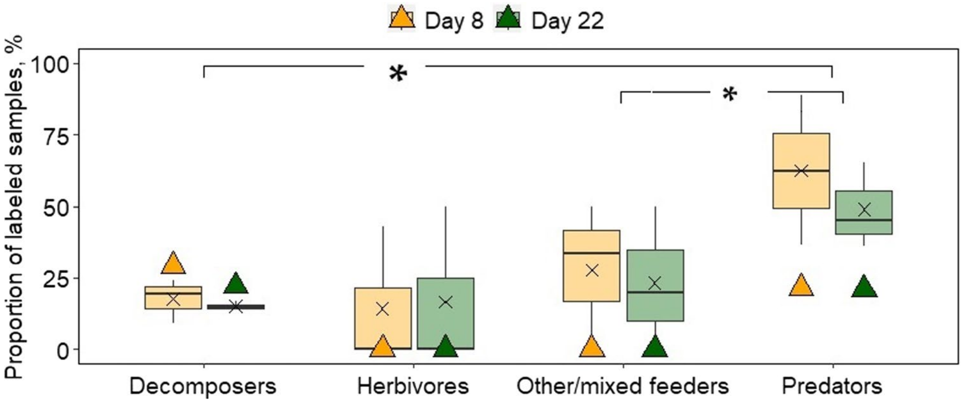


Fig. 1 Proportion of labeled samples of soil animals (P_L) on days 8 and 22 after the addition of ^{15}N-labeled collembolans. Boxplots show median value, interquartile range, and minimum and maximum values for the + Coll treatment ($n = 3$); x-symbols show mean values. There were no differences between days in all groups. Predators differed from decomposers ($P = 0.03$) and other/mixed feeders ($P = 0.03$). Triangles show P_L values for the + dColl treatment ($n = 1$). Parasitoids did not receive the isotopic label ($P_L = 0$)

and 4.8%, respectively). This tendency was much less pronounced in herbivores and mixed feeders (Supplementary Fig. S2).

Consumption of living and dead Collembola by individual taxa of soil animals

Across two sampling events, the isotopic label in the + Coll treatment was found most often in the mesopredators Trombidiformes ($P_L = 83.3 \pm 16.7\%$; $\delta^{15}N_L$ 165 [115.2–628.6]‰) and Mesostigmata mites ($P_L = 85 \pm 8.9\%$; $\delta^{15}N_L$ 79.5 [9.2–624.9]‰), followed by macropredators Araneae ($P_L = 57.8 \pm 9.2\%$; $\delta^{15}N_L$ 79.3 [7.0–223.9]‰), Chilopoda ($P_L = 45.2 \pm 4.8\%$; $\delta^{15}N_L$ 38.6 [7.9–552.7]‰), and Coleoptera ($P_L = 29.4 \pm 0.4\%$; $\delta^{15}N_L$ 33.2 [7.6–475.1]‰) (Fig. 2, Supplementary Table S3). Among non-predatory groups the isotopic label was most often recorded in herbivorous Thysanoptera ($P_L = 26.7 \pm 26.7\%$; $\delta^{15}N_L$ 9.4 [3.9–43.5]‰), and decomposer Collembola ($P_L = 23.8 \pm 13.4\%$; $\delta^{15}N_L$ 12.8 [5.7–33.9]‰) and Oribatida ($P_L = 18 \pm 0.9\%$; $\delta^{15}N_L$ 15.5 [2.7–81.1]‰). The ^{15}N-label was also detected in Symphyla, Formicidae, Diplura, Diplopoda, Opiliones, Diptera, Hemiptera, Oligochaeta, and Nematoda.

In the + dColl treatment, the proportion of ^{15}N-labeled samples was lower. The label was found most often in Mesostigmata ($P_L = 35.7\%$; $\delta^{15}N_L$ 21.7 [8.7–194.5]‰), Oribatida ($P_L = 25.2\%$; $\delta^{15}N_L$ 15.3 [2.5–111.7]‰), Araneae ($P_L = 31.3\%$; $\delta^{15}N_L$ 21.3 [7.9–81.2]), and Coleoptera ($P_L = 18.2\%$; $\delta^{15}N_L$ 9.3 [8.6–12.2]‰). In Collembola, the label was detected only in one out of 8 samples ($\delta^{15}N_L$: 27.2‰), while four labeled earthworms (out of 11 measured) were found in the + dColl treatment. A complete list of ^{15}N-labeled samples is given in Supplementary Table S3.

The proportion of labeled samples in different taxa of soil animals in the + Coll treatment was positively correlated with the mean natural δ^{15}N values of the corresponding family, indicating that the probability of consuming labeled collembolans increased with the increase in the trophic level. This correlation was significant in predators, but not in decomposers (Fig. 3).

Discussion

Consumption of live Collembola by soil animals

Our results suggest that the flux of invertebrates falling from the canopy to the soil surface can significantly contribute to the energy budget of soil animals. Collembola species *Folsomia candida* which represented arthropod rain in our experiment was chosen because this species could be easily maintained on the ^{15}N-labelled artificial diet. However, it should be noted that this species is not typical of the soil or canopy fauna at the study site. Moreover, *F. candida* contains toxins that may be poisonous to predators. Several experiments demonstrated that feeding on *F. candida* reduced the survival and growth rate of spiders (Toft and Wise 1999; Oelbermann and Scheu 2002),

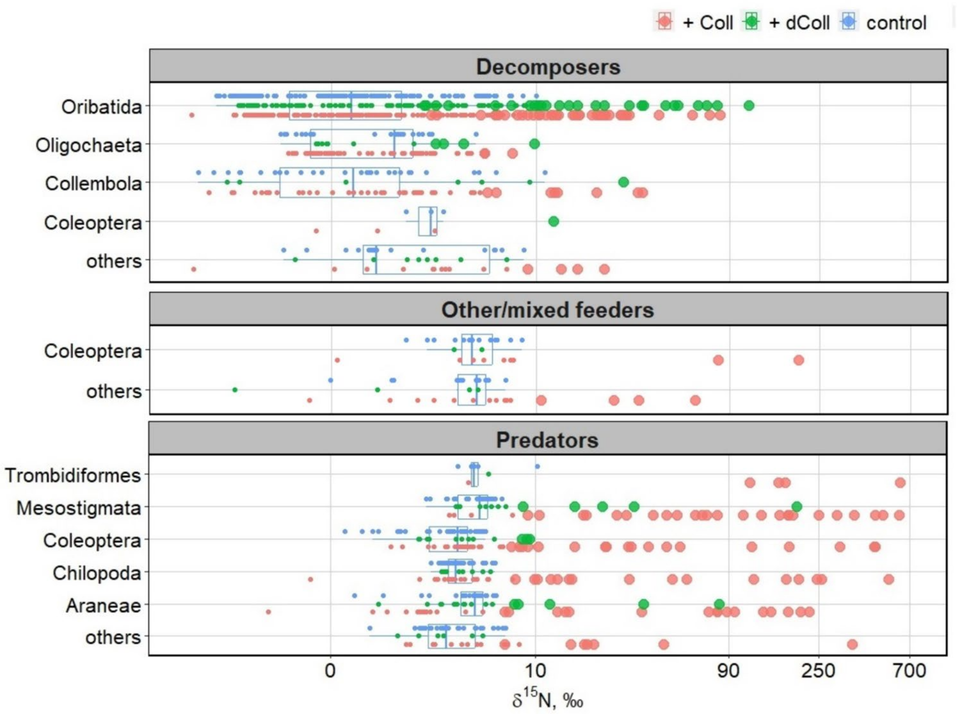
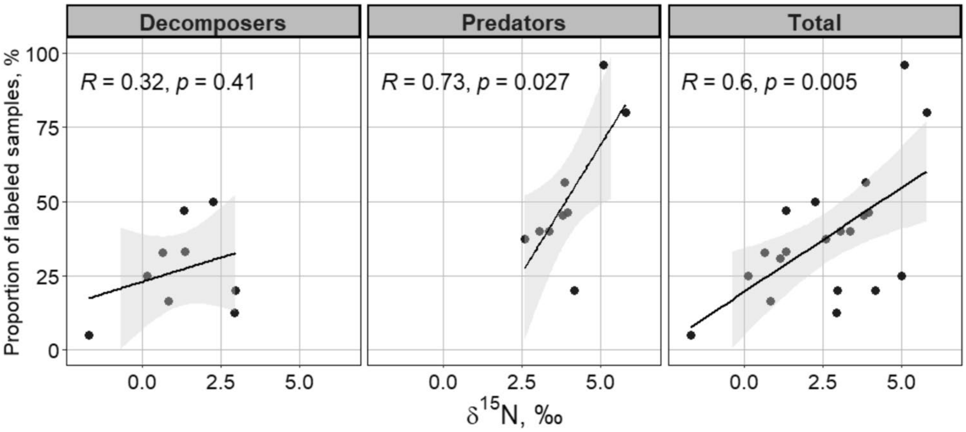


Fig. 2 Distribution of the δ^{15}N values of the most abundant taxa of soil animals after the addition of ^{15}N-labeled collembolans. Data from two sampling events (days 8 and 22) are combined. Boxplots show the median value and interquartile range in non-labeled samples from the control treatment (blue dots). In the labeled treatments (red and green dots), smaller and larger symbols show individual non-labeled and labeled samples, respectively. The threshold separating labeled and unlabeled samples was identified separately for each family or genus (see Table S3). Note that the number of samples processed was ca. three times larger in + Coll than + dColl treatments (582 and 225 samples, respectively)

Fig. 3 Proportion of labeled samples after the addition of ^{15}N-labeled living collembolans (+Coll treatment) as related to the mean natural δ^{15}N values of the corresponding taxon (family). In the left panels, decomposers and predators are shown separately for clarity. Two samplings (days 8 and 22) are combined. Only the most abundant ($n > 4$) groups of soil animals are shown



although spiders are seemingly unable to develop an aversion against this prey (Fisker and Toft 2004). Thus, our model collembolan species represented low-quality prey and were likely not more attractive to soil predators than other soil invertebrates.

As we suggested in Hypothesis 1, the simulated arthropod rain was readily consumed by a wide range of soil invertebrates. The ^{15}N-label was detected in about 24% of the tissue samples of soil invertebrates belonging to all major trophic groups, except for parasitoids, and to more than 30 taxonomic groups (family level) of soil meso- and macrofauna. The proportion of the labeled samples was higher at the first sampling (Supplementary Table S2) indicating the rapid consumption of living Collembola both by predators and decomposers.

Overall, the distribution of the label among soil organisms of different taxonomic and trophic groups followed an expected pattern (Potapov et al. 2022). The label was found in all main groups of predators, including mites, spiders, centipedes, and predatory beetles. Collembolans are regular prey for litter- and aboveground-dwelling spiders and carabids serving as a "detrital subsidy" that supports aboveground food webs (Johnston 2000; Halaj and Wise 2002; Zuev et al. 2020). Chilopods in our samples were represented mainly by Lithobiidae which are among the most active hunters of springtails in the soil and litter layer (Lewis 2006). This is confirmed by the high P_L values and occasionally very high δ^{15}N values of labeled specimens. Notably, Chilopoda did not seem to consume dead springtails (Fig. 2, Fig. 4; Table S3).

Less anticipated was a relatively frequent consumption of live collembolans by several decomposer taxa, especially Oribatida mites, but also Collembola and Symphyla. The label was also found in Thysanoptera, herbivores with sucking mouthparts. Moreover, the label sporadically occurred in millipedes and enchytraeids. Omnivory is widespread in soil food webs (Chernova et al. 2007; Wang et al. 2022), thus the appearance of the ^{15}N-label in these groups is not surprising. Still, it indicates that some trophic connections in the detrital food webs can be underestimated.

The size channels hypothesis

The size channels hypothesis suggests that soil food webs are compartmentalized according to the body size of the organisms with the interaction within each size group (e.g. mesofauna) being more intense than between size groups (e.g. between mesofauna and macrofauna) (Potapov et al. 2021; Potapov 2022). We, therefore, expected that mesopredators having a body size comparable to collembolans would receive the label more often than larger macropredators. Indeed, the highest δ^{15}N values (exceeding 600‰) and a high frequency of label was observed in Mesostigmata and Trombidiformes. Overall, in the + Coll treatment mesofauna predators were more often labelled than macropredators, and the same pattern was observed in decomposers (Fig. S2).

This conclusion, however, is not robust. The P_L values of the small-sized mesopredators, such as mesostigmatid mites, could be overestimated because each sample analyzed usually contained several individuals. The label threshold was set quite low, thus the whole sample was considered labeled if it contained a single strongly labeled individual. On the other hand, the isotopic label could be diluted in the large bodies of macrofauna species. As a result, the distribution of the δ^{15}N values in labeled mesopredators (e.g. Mesostigmata) and macropredators (e.g. Chilopoda) was similar (Fig. 2).

Consumption of live and dead Collembola by predators and decomposers

According to our Hypothesis 2, live Collembola were consumed mainly by predators, thereby acting as an aboveground subsidy that primarily supports organisms of the higher trophic levels. In this respect, arthropod rain is very different from other types of organic matter inputs from the

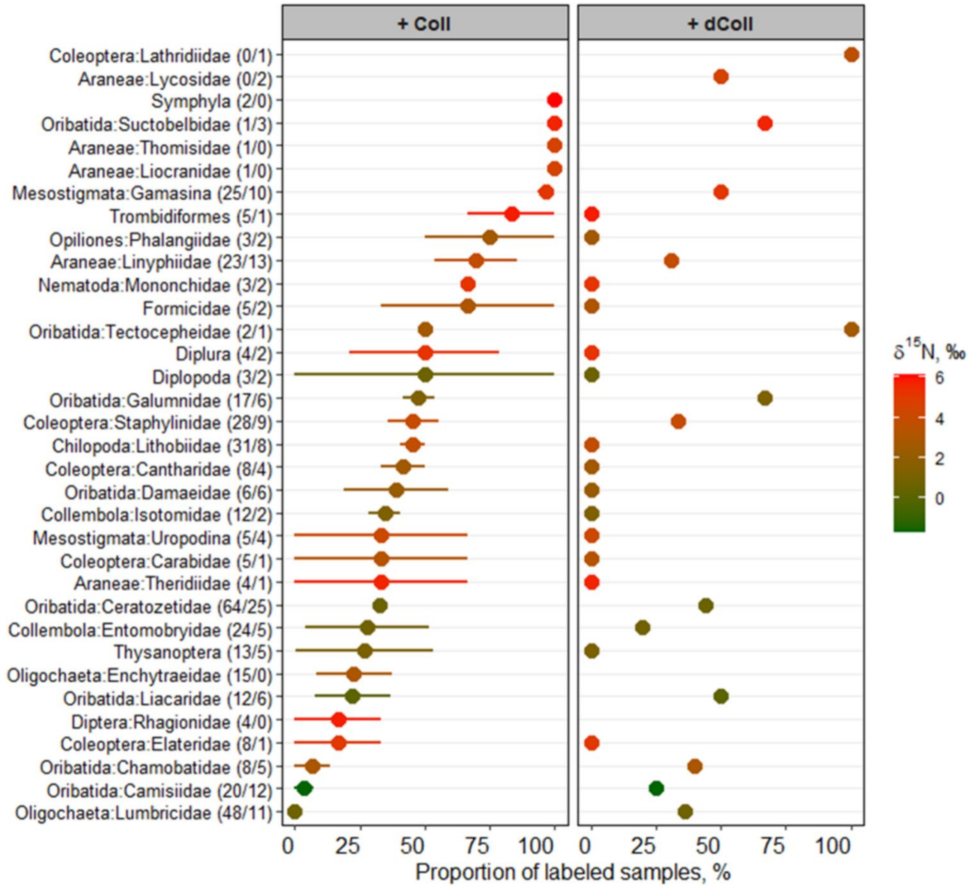


Fig. 4 Proportion of labeled samples (P_L values) in separate taxa (usually families) of soil animals after the addition of ^{15}N-labeled collembolans ($n = 3$ for + Coll, $n = 1$ for + dColl). Data from two sampling events (days 8 and 22) are combined. Colors show mean natural δ^{15}N values from the control treatment. Numbers in brackets show the total amount of samples analyzed in the + Coll and + dColl treatments, respectively. Whiskers show 1 SE

forest canopy, such as leaf litter or honeydew, that end up at the base of the detrital food web.

It is not known to what extent the support of soil predators may affect key functions and parameters of the soil food web, such as the abundance of decomposers and the rate of litter decomposition. It is usually assumed that soil arthropod communities are rarely top-down controlled (Kajak 1995; Wardle 2002; Goncharov and Tiunov 2014). However, our experiment confirmed a high predation pressure on collembolans, which was suggested (Johnston 2000) but rarely shown experimentally in field conditions (e.g. Lawrence and Wise 2000; Wise 2004).

We previously suggested that arthropod rain is sufficient to cover most of the food requirements of spiders at the study site (Rozanova et al. 2019). However, field experiments with spiders and other predators showed both a positive (Lawrence and Wise 2004; Melguizo-Ruiz et al. 2020) and negative (Lawrence and Wise 2000; Liu et al. 2014) or neutral (Miyashita and Niwa 2006) relationship between the abundance of predators and the rate of litter decomposition. Moreover, arthropod rain is also consumed by saprophages, making its impact on decomposition even more difficult to predict. However, in general, arthropod rain can be considered as an addition of animal protein to the soil system. This should accelerate litter decomposition and nutrient cycling (Hawlena et al. 2012).

Natural arthropod rain includes not only live animals but also dead animals and their derivates like exuviae. This dead component makes up about 28% of the total biomass of the arthropod rain and can be easily consumed by various trophic groups of soil fauna, including saprophages and herbivores. To this end, we included the + dColl treatment in our experiment. Even though this treatment was not replicated, the data obtained confirm that dead collembolans are directly or indirectly consumed by a wide range of soil saprophages, including Collembola, Coleoptera, Lumbricidae, and especially oribatid mites.

Due to the high intensity of the consumption of the dead springtails by oribatids (Fig. 2), the proportion of labeled samples in detritivores was higher in the + dColl than in the + Coll treatment, being comparable to the consumption of the dead collembolans by predators (Fig. 1). Oribatid mites are trophic generalists that occupy several trophic levels and include predators and scavengers (Rockett and Woodring 1966; Schneider et al. 2004). The ^{15}N-label was especially often found in Ceratozetidae and Galumnidae; about half of the samples were labeled, with the P_L values higher when dead Collembola were added (Fig. 4).

On the other hand, the $\delta^{15}N$ values in the labeled oribatids did not exceed 90‰ (versus 600 + ‰ in predatory mites of comparable size) indicating another feeding mode. The isotopic label could enter soil food webs in many ways. Very high $\delta^{15}N$ values in some predators obviously indicated direct predation (Fig. 2), but the consumption of exuviae, or feces of predators could also take place. In particular, we found several labeled earthworms, which is consistent with the idea that large saprophages are "ecosystemivores" consuming indiscriminately the whole soil matrix and its small-sized inhabitants (Pokarzhevskii et al. 1997). Moreover, the consumption of labeled collembolans (P_L values) correlated with the $\delta^{15}N$ values in the predatory animals, but not in the decomposers (Figs. 3, 4). This pattern suggests that specialized scavengers or opportunistic predators are rare among decomposers.

Thus, we showed that in addition to the detrital subsidy that supports aboveground generalist predators (Halaj and Wise 2002; Miyashita et al. 2003), herbivores and saprophages falling from the crowns form "aboveground subsidy" that can support a wide range of animals in the forest soil. This phenomenon is well known only for the soil animal communities inhabiting habitats poor in indigenous resources, such as glacier forelands or volcanic ashes (Hodkinson et al. 2001, 2002). Our results suggest that the aboveground subsidy is a much more widespread phenomenon.

In our analysis, the isotopic threshold separating labeled and non-labeled animals was deliberately set low enough to detect the label in decomposers that received it indirectly, e.g. feeding on the feces of predators. Thus, the proportion of labeled animals could have been slightly overestimated, which, however, does not affect our main conclusions. On the other hand, in this experiment we added only a tiny amount of live or dead biomass, equivalent to the daily dose of the arthropod rain (19 mg d.w. m^{-2} day^{-1}), while the total flux across the whole season averaged about 3.8 g d.w. m^{-2}. Moreover, we added a single prey of uncertain trophic quality, while the arthropod rain consists of many taxa, including seemingly palatable prey such as aphids and dipteran larvae (Rozanova et al. 2019). In more natural settings, the contribution of the arthropod rain to the diet of soil animals can be much larger.

Conclusions

Our study contributes to an emerging view that soil food webs are not entirely "detrital" but receive a large part of their energy from green plants. Unlike other forms of aboveground subsidy of the soil food webs, including leaf litter, root exudates, mycorrhiza, frass, honeydew, etc., that are primarily processed by microorganisms, arthropod rain is assimilated directly by the animals, supporting especially high-order consumers. We found an unexpectedly high frequency of the inclusion of the aboveground subsidy in a forest soil food web, suggesting that this source of energy and nutrients can make a major contribution to maintaining the abundance (and possibly diversity) of soil predators.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-024-05595-y.

Acknowledgements This study was supported by the Russian Science Foundation, project no. 22-14-00363. AAK was supported by state assignment of the Institute of Biology, Komi Scientific Centre, Ural Branch, Russian Academy of Sciences, no. 122040600025-2. We thank Eugenia Semenina for the help in the laboratory work. Dr. Jacob D. Wickham (IEE RAS) kindly improved the English of the manuscript.

Author contribution statement OLR and AVTiunov conceived and designed the study. OLR, SMT, AAK, VDL, MGK, DNF, AVTanasevitch, and LBR conducted fieldwork and identified animals. SMT performed isotopic analysis. OLR analyzed the data and made the figures. OLR and AVTiunov wrote the manuscript, and all authors reviewed and contributed to the final text. AVTiunov, SMT, and OLR obtained funding.

Funding Russian Science Foundation, project 22–14-00363.

Data availability Full datasets used in the current study is available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All applicable institutional and national guidelines for the use of animals were followed.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Bardgett RD, Wardle DA, Yeates GW (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biol Biochem 30:1867–1878. https://doi.org/10.1016/S0038-0717(98)00069-8

Baxter CV, Fausch KD, Carl Saunders W (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw Biol 50:201–220. https://doi.org/10.1111/j.1365-2427.2004.01328.x

Chan EKW, Zhang Y, Dudgeon D (2008) Arthropod "rain" into tropical streams: the importance of intact riparian forest and influences on fish diets. Mar Freshw Res 59:653–660. https://doi.org/10.1071/MF07191

Chernova NM, Bokova AI, Varshav EV et al (2007) Zoophagy in Collembola. Entomol Rev 87:799–811. https://doi.org/10.1134/S0013873807070020

Fisker EN, Toft S (2004) Effects of chronic exposure to a toxic prey in a generalist predator. Physiol Entomol 29:129–138. https://doi.org/10.1111/j.1365-3032.2004.00376.x

Goncharov AA, Tiunov AV (2014) Trophic chains in the soil. Biol Bull Rev 4:393–403. https://doi.org/10.1134/S207908641405003X

Goncharov AA, Tsurikov SM, Potapov AM, Tiunov AV (2016) Short-term incorporation of freshly fixed plant carbon into the soil animal food web: field study in a spruce forest. Ecol Res 31:923–933. https://doi.org/10.1007/s11284-016-1402-7

Gongalsky KB (2021) Soil macrofauna: study problems and perspectives. Soil Biol Biochem 159:108281. https://doi.org/10.1016/j.soilbio.2021.108281

Halaj J, Wise DH (2002) Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. Ecology 83:3141–3151. https://doi.org/10.1890/0012-9658(2002)083[3141:IOADSO]2.0.CO;2

Hawlena D, Strickland MS, Bradford MA, Schmitz OJ (2012) Fear of predation slows plant-litter decomposition. Science 336(6087):1434–1438. https://doi.org/10.1126/science.1220097

Hodkinson ID, Coulson SJ, Harrison J, Webb NR (2001) What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic—some counter-intuitive ideas on community assembly. Oikos 95:349–352. https://doi.org/10.1034/j.1600-0706.2001.950217.x

Hodkinson ID, Webb NR, Coulson SJ (2002) Primary community assembly on land—the missing stages: why are the heterotrophic organisms always there first? J Ecol 90:569–577. https://doi.org/10.1046/j.1365-2745.2002.00696.x

Hood-Nowotny R, Knols BGJ (2007) Stable isotope methods in biological and ecological studies of arthropods. Entomol Exp Appl 124:3–16. https://doi.org/10.1111/j.1570-7458.2007.00572.x

IUSS WRB (2014) World reference base for soil resources 2014. International soil classification system for naming soils and creating legends for soil maps. Food and Agriculture. Organization of the United Nations. Rome.

Jochum M, Eisenhauer N (2022) Out of the dark: using energy flux to connect above- and belowground communities and ecosystem functioning. Eur J Soil Sci 73:e13154. https://doi.org/10.1111/ejss.13154

Johnston JM (2000) The contribution of microarthropods to aboveground food webs: a review and model of belowground transfer in a coniferous forest. Am Midl Nat 143:226–238. https://doi.org/10.1674/0003-0031(2000)143[0226:TCOMTA]2.0.CO;2

Kajak A (1995) The role of soil predators in decomposition processes. Eur J Entomol 92:573–580

Kawaguchi Y, Nakano S (2001) Contribution of terrestrial invertebrates to the annual resource budget for Salmonids in forest and grassland reaches of a headwater stream: Riparian prey contribution to salmonids. Freshw Biol 46:303–316. https://doi.org/10.1046/j.1365-2427.2001.00667.x

Lawrence KL, Wise DH (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44:33–39

Lawrence KL, Wise DH (2004) Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. Pedobiologia 48:149–157. https://doi.org/10.1016/j.pedobi.2003.11.001

Lewis JGE (2006) The biology of centipedes. Cambridge University Press

Liu S, Chen J, He X et al (2014) Trophic cascade of a web-building spider decreases litter decomposition in a tropical forest floor. Eur J Soil Biol 65:79–86. https://doi.org/10.1016/j.ejsobi.2014.10.004

Macdonald DW (1983) Predation on earthworms by terrestrial vertebrates. In: Satchell JE (ed) Earthworm ecology. Chapman and Hall, pp 393–414

Martay B, Pearce-Higgins JW (2020) Opening a can of worms: can the availability of soil invertebrates be indicated by birds? Ecol Indic 113:106222. https://doi.org/10.1016/j.ecolind.2020.106222

Melguizo-Ruiz N, Jimenez-Navarro G, De Mas E et al (2020) Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. J of Anim Ecol 89:334–346. https://doi.org/10.1111/1365-2656.13101

Milcu A, Bonkowski M, Collins CM, Crawley MJ (2015) Aphid honeydew-induced changes in soil biota can cascade up to tree crown architecture. Pedobiologia 58:119–127. https://doi.org/10.1016/j.pedobi.2015.07.002

Miyashita T, Niwa S (2006) A test for top-down cascade in a detritus-based food web by litter-dwelling web spiders. Ecol Res 21:611–615. https://doi.org/10.1007/s11284-006-0155-0

Miyashita T, Takada M, Shimazaki A (2003) Experimental evidence that aboveground predators are sustained by underground detritivores. Oikos 103:31–36. https://doi.org/10.1034/j.1600-0706.2003.12586.x

Müller J, Brandl R, Brändle M et al (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 594:814–824. https://doi.org/10.1111/oik.04972

Oelbermann K, Scheu S (2002) Effects of prey type and mixed diets on survival, growth and development of a generalist predator, *Pardosa lugubris* (Araneae: Lycosidae). Basic Appl Ecol 3:285–291. https://doi.org/10.1078/1439-1791-00094

Pokarzhevskii AD, Zaboyev DP, Ganin GN, Gordienko SA (1997) Amino acids in earthworms: are earthworms ecosystemivorous? Soil Biol Biochem 29:559–567. https://doi.org/10.1016/S0038-0717(96)00180-0

Polis GA, Strong DR (1996) Food web complexity and community dynamics. Am Nat 147:813–846. https://doi.org/10.1086/285880

Potapov AM (2022) Multifunctionality of belowground food webs: resource, size and spatial energy channels. Biol Rev 97:1691–1711. https://doi.org/10.1111/brv.12857

Potapov AM, Goncharov AA, Tsurikov SM et al (2016) Assimilation of plant-derived freshly fixed carbon by soil collembolans: Not only via roots? Pedobiologia 59:189–193. https://doi.org/10.1016/j.pedobi.2016.07.002

Potapov AM, Scheu S, Tiunov AV (2019a) Trophic consistency of supraspecific taxa in below-ground invertebrate communities: comparison across lineages and taxonomic ranks. Funct Ecol 33:1172–1183. https://doi.org/10.1111/1365-2435.13309

Potapov AM, Tiunov AV, Scheu S (2019b) Uncovering trophic positions and food resources of soil animals using bulk natural stable isotope composition: stable isotopes in soil food web studies. Biol Rev 94:37–59. https://doi.org/10.1111/brv.12434

Potapov AM, Rozanova OL, Semenina EE et al (2021) Size compartmentalization of energy channeling in terrestrial belowground food webs. Ecology 102:e03421. https://doi.org/10.1002/ecy.3421

Potapov A, Beaulieu F, Birkhofer K et al (2022) Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. Biol Rev 97:1057–1117. https://doi.org/10.1111/brv.12832

Pringle RM, Fox-Dobbs K (2008) Coupling of canopy and understory food webs by ground-dwelling predators. Ecol Lett 11:1328–1337. https://doi.org/10.1111/j.1461-0248.2008.01252.x

Ritzenthaler CA, Maloney CE, Maran AM et al (2018) The feedback loop between aboveground herbivores and soil microbes via deposition processes. In: Ohgushi T, Wurst S, Johnson SN (eds) Aboveground-Belowground Community Ecology. Springer, Cham, pp 201–221

Rockett CL, Woodring JP (1966) Oribatid mites as predators of soil nematodes. Ann Entomol Soc Am 59:669–671. https://doi.org/10.1093/aesa/59.4.669

Rozanova OL, Tsurikov SM, Tiunov AV, Semenina EE (2019) Arthropod rain in a temperate forest: intensity and composition. Pedobiologia 75:52–56. https://doi.org/10.1016/j.pedobi.2019.05.005

Rozanova OL, Tsurikov SM, Krivosheina MG et al (2022) The isotopic signature of the "arthropod rain" in a temperate forest. Sci Rep 12:321. https://doi.org/10.1038/s41598-021-03893-6

Scheu S (2001) Plants and generalist predators as links between the below-ground and above-ground system. Basic Appl Ecol 2:3–13. https://doi.org/10.1078/1439-1791-00031

Schneider K, Migge S, Norton RA et al (2004) Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios (15N/14N). Soil Biol Biochem 36:1769–1774. https://doi.org/10.1016/j.soilbio.2004.04.033

Schowalter TD, Crossley DA (1983) Forest canopy arthropods as sodium, potassium, magnesium and calcium pools in forests. For Ecol Manag 7:143–148. https://doi.org/10.1016/0378-1127(83)90026-9

Seeger J, Filser J (2008) Bottom-up down from the top: Honeydew as a carbon source for soil organisms. Eur J Soil Biol 44:483–490. https://doi.org/10.1016/j.ejsobi.2008.07.008

Striganova BR (1980) Nutrition of Soil Saprophages. Nauka, Moscow

Toft S, Wise DH (1999) Behavioral and ecophysiological responses of a generalist predator to single-and mixed-species diets of different quality. Oecologia 119:198–207. https://doi.org/10.1007/s004420050777

Van der Putten WH, Bardgett RD, de Ruiter PC et al (2009) Empirical and theoretical challenges in aboveground–belowground ecology. Oecologia 161:1–14. https://doi.org/10.1007/s00442-009-1351-8

Wallwork JA (1970) Ecology of soil animals. McGraw-Hill, London

Wang Z, Mound LA, Hussain M et al (2022) Thysanoptera as predators: their diversity and significance as biological control agents. Pest Manag Sci 78:5057–5070. https://doi.org/10.1002/ps.7176

Wardle DA (2002) Communities and ecosystems: linking the above ground and below ground components. Princeton University Press

Wardle DA (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633. https://doi.org/10.1126/science.1094875

Wise DH (2004) Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48:181–188. https://doi.org/10.1016/j.pedobi.2003.12.001

Zuev A, Heidemann K, Leonov V et al (2020) Different groups of ground-dwelling spiders share similar trophic niches in temperate forests. Ecol Entomol 45:1346–1356. https://doi.org/10.1111/een.12918