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Non-vascular plants as a food source for litter-dwelling Collembola: Field evidence

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S U M M A R Y

Non-vascular plants such as mosses, lichens and especially microalgae are widespread in terrestrial ecosystems, but their contribution in the nutrient cycling and energy budget of soil food webs is generally neglected. Despite a relatively low total biomass, soil microalgae can be very productive and contribute to the diet of many soil decomposers such as Collembola. Using $^{15}N/^{14}N$ ratios we showed that phycophagy is of particular importance for Collembola in extreme habitats like rock surfaces, or seasonally during the wintertime. In such situations, non-vascular plants can represent the major part of the diet of Collembola. In a temperate spruce forest partial phytophagy was observed for epigeic collembolan species. These species account for about half of the total biomass of litter-dwelling springtails. Experimental blackout of the forest floor affected population density and species richness of Collembola along with their $\delta^{15}N$ values, confirming the importance of soil microalgae for maintaining the structure of collembolan communities. These results support the emerging view that soil phototrophic microorganisms should be considered an important channel for nutrient cycling in soil communities.

1. Introduction

Principal carbon sources forming the base of soil food webs are plant residues, soil organic matter, and exudates from living root (de Ruiter et al., 1995; Goncharov and Tiunov, 2012; Pollierer et al., 2007). In addition, photoautotrophic soil microorganisms play a considerable role in the nutrition of soil animals including Collembola (Schmidt et al., 2016). Biotic interactions between Collembola and non-vascular plants (NVP), such as algae, bryophytes and lichens, are explored in several studies (Aptroot and Berg, 2004; Cronberg et al., 2006; Rosenstiel et al., 2012). Among NVP, algae are seemingly the most palatable food source for springtails. Collembola readily consume algae in laboratory culture (Buse et al., 2013; Buse and Filser, 2014) and benefit from algae added to fungal diet (Scheu and Folger, 2004; Verhoef et al., 1988). Algae and lichen are especially important as a basal food source for springtails in certain types of extreme habitats. For instance, species inhabiting alpine rocks (Leinaas and Fjellberg, 1985; Leinaas and Sømme, 1984) or the snow surface (Hagvar, 2000; Zettel, 2010; Zhang et al., 2014) are likely to feed on non-vascular plants. Moreover, in nival or subnival ecosystems, algae and lichens serve as a source of antifreezes for microarthropods (Bokhorst et al., 2007; Sømme, 1982; Worland and Lukešová, 2000).

In temperate forests, abundant algal populations can be found in the upper litter layers, on tree trunks and other illuminated surfaces. Nevertheless, the abundance and biomass of microscopic algae in temperate forest soils is relatively low in comparison to bacteria and fungi, typically about 10^5 cells g^{-1} and ca. 20–30 kg ha^{-1} (Aleksakhina and Shtina, 1984; Hunt et al., 1979; Kabirov and Gaisina, 2009; Siemniak, 1996). However, soil algae can have great productivity (Metting, 1981; Starks et al., 1981). The production of soil algae is difficult to measure in the field but estimates range from several to several hundred kg ha^{-1} yr^{-1} (Kabirov and Gaisina, 2009; Siemniak, 1996; Szanser et al., 2011). Many collembolan species developed adaptations to a life above ground, e.g. long antennae and good visual system, and can easily access aboveground NVP and algae in particular (Rusek, 2007), whereas hemiedaphic species can consume microscopic algae while grazing on plant litter (Ponge, 2000). Nevertheless, soil algae and other non-vascular plants are rarely considered as one of the principal components of collembolan diet in forest ecosystems. So far, only a few studies recognized soil algae as an important basal resource for soil food webs (Schmidt et al., 2016; Seppey et al., 2017).

Non-vascular plants obtain nitrogen via N_2-fixation or intercepting ^{15}N-depleted nitrogen from wet and dry atmospheric depositions (Dahlman et al., 2004; Harmens et al., 2011; Schröder et al., 2010). This results in a typically low $^{15}N/^{14}N$ isotopic ratio (Delgado et al., 2013; Solga et al., 2005; Tozer et al., 2005). Consequently, microarthropod

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species with $\delta^{15}N$ values below those of the litter were assigned to the algae/lichen feeder guild existing among oribatid mites (Schneider et al., 2004) and springtails (Chahartaghi et al., 2005). At least 20% of collembolan species in temperate forests are depleted in ^{15}N relative to the litter which suggests that they are trophically linked to NVP (Potapov et al., 2016). This is a tentative conservative estimate since microarthropods are expected to be enriched in ^{15}N relative to their food due to trophic fractionation (Post, 2002; Potapov et al., 2013).

In this study we estimated how common phycophagy is among collembolan species inhabiting extreme habitats and a temperate spruce forest. To this end, we analyzed $^{15}N/^{14}N$ ratios ($\delta^{15}N$ values) of springtails, litter and NVP (lichens or algae). Furthermore, in an *in situ* experiment we studied the response of collembolan species to blacking out the soil surface. Blacking out presumably reduces photosynthetic activity of NVP. We hypothesized (1) that there would be an increase in $\delta^{15}N$ values but a reduction in Collembola abundance in the blacked out plots. We also expected that (2) this trend will be more pronounced for species living in the upper-litter (atmobiotic and epedaphic life forms) than for those living in the lower-litter (hemiedaphic life form).

2. Material and methods

2.1. Material collecting and processing

Rocks and snow surfaces were chosen as an example of extreme habitats where NVP can serve as an important food source for Collembola. Several sandstone outcrops (ca. 15–30 m in height) covered with lichens and surrounded by beech forest were inspected in September 2014 in Saxon Switzerland, Germany (Location A, 50°54′18“N 14°13′09“E, Fig. 1A). Lithobiont springtails (*Orchesella alticola*) from the rock surfaces were collected non-quantitatively with an entomological aspirator and fixed immediately in 70% ethanol. Lichens were scratched off with a knife and freshly fallen beech leaves were collected near the base of the rocks to estimate the isotopic baseline. Collembola from the snow surfaces were collected in February and March 2016 in a *Salix* grove in Moscow region, Russia (Location B, 55°58′31“N 35°36′01“E, Fig. 1 B). High densities (thousands ind. m^{-2}) of winter-migrating *Hypogastrura socialis* were observed in depressions. *Isotoma viridis* and *Desoria hiemalis* were also present on the flat snow areas between the trees although in lower densities. Springtails were collected non-quantitatively with an entomological aspirator and fixed immediately in 70% ethanol. Along with springtails, two unidentified morphotypes of lichens and mosses were scratched off nearby tree trunks with a knife. To estimate the isotopic baseline, litter of *Salix caprea* was taken from under the snow (the snow cover was 10–15 cm in thickness).

Litter-dwelling Collembola were collected in a spruce forest at the Malinky biological station in Moscow region, Russia (Location C, 55°27′30“N 37°10′41“E, Fig. 1C). Twelve samples of leaf litter (25 × 25 cm) were taken in October 2014. (These samples were also used as a control for the blackout experiment, see below). In the same spruce forest, lichens were collected in 2014 monthly (every 25-28 days) from June 20 to October 6. On each sampling occasion, three samples of lichens were scratched off with a knife from the surfaces of three neighboring spruce trunks at heights of 0.5, 1 and 1.5 m above the ground (9 samples per date, in total 45 samples). To get more information about the stable isotope composition of NVP, algae were also collected from the tree trunks in a nearby riparian alder forest following the same sampling scheme (n = 45, Location D, distance of ca. 500 m from the Location C). Lichens from the spruce forest were represented largely by soredia or juvenile talli of *Hypogimnia physodes* and *Parmelia sulcata*, whereas green algae were identified as *Trentepohlia* sp.

2.2. Ground-blackout experiment

The experiment was conducted in June-October 2014 in the spruce forest (Location C). Two pairs of blackout and control plots were established. Each plot was 5 × 5 m and the distance between pairs was 100 m. Blackout plots were covered with two layers of the black polyethylene film (thickness 0.15 mm, Mostorg, Russia). The film was perforated with a knife to ensure air exchange and inflow of rainwater. Cuts ca. 5 cm in length were made forming a square grid with 20 cm intervals. After 105 days, the film was removed and six samples of litter (25 × 25 cm) from each control and blackout plot were taken near the center of the plot to extract Collembola (in total, 24 samples). Samples of litter (L horizon) were taken from each plot to estimate the isotopic baseline (n = 5-6). The ground vegetation in the blackout plots was strongly suppressed at the end of the experiment except for sparse mosses (Fig. 2).

Animals from the litter were extracted into 70% ethanol using

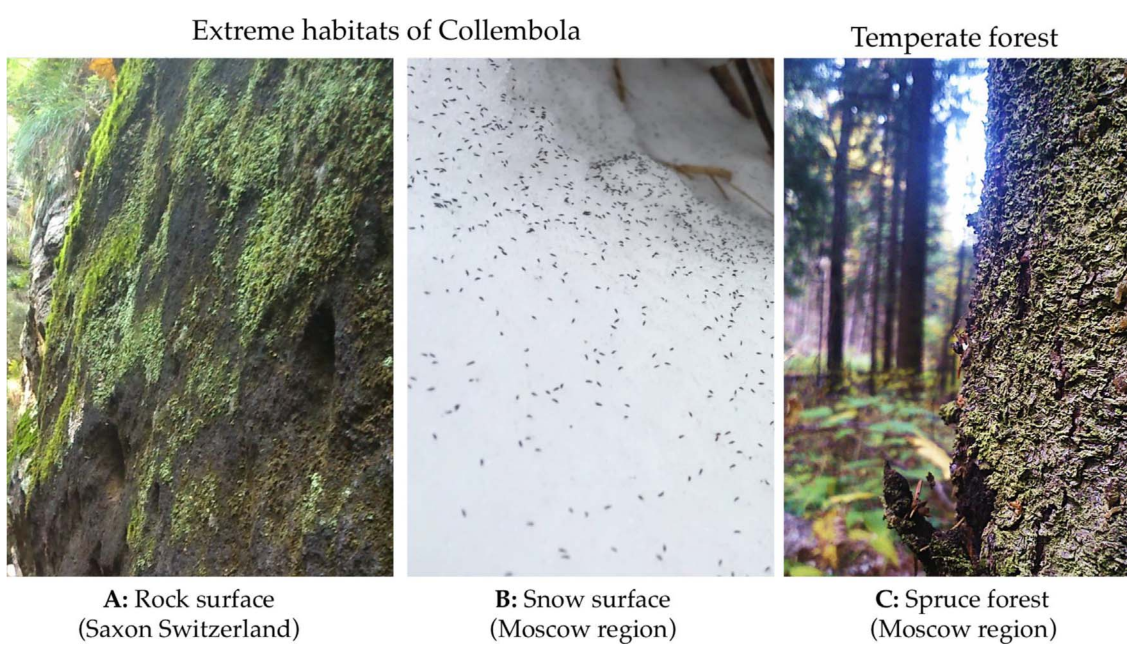

Fig. 1. Study sites. Locations A and B: extreme habitats of Collembola, rock surface colonized by lichens in Saxon Switzerland and snow surface with *Hypogastrura socialis* (Hypogastruridae) in Moscow region. Location C: tree trunk in a temperate spruce forest in Moscow region.