



Vascular plant litter input in subarctic peat bogs changes Collembola diets and decomposition patterns

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ABSTRACT

In high-latitude ecosystems climate change induced plant community shifts toward dominance of shrubs and trees will potentially have large consequences for soil carbon dynamics. Changes in the litter layer due to an altered quantity and quality of litter input, or by its indirect effect on the microclimate, might affect the decomposer community.

To be able to predict the effects of increased litter input on decomposers and consequently on soil carbon dynamics, we studied the contribution of Collembola to carbon processing in a high-latitude peat bog system. Moreover, we assessed the effects of changing litter inputs on their abundance, diversity and diet choice, using a ^{13}C tracer approach.

The $\delta^{13}\text{C}$ signatures of Collembola in peat moss (*Sphagnum fuscum*) showed that species differed in their diet. However, when vascular plant litter (*Betula pubescens*) entered the *Sphagnum* peat ecosystem, the $\delta^{13}\text{C}$ signatures of the Collembola, changed and species-specific differences disappeared. There were no significant changes in Collembola species composition and density after *Betula* litter addition, but all species showed a strong dietary preference for *Betula*-associated food sources over *Sphagnum*; 67% of their diet contained carbon originating from *Betula* litter. Decomposition patterns corresponded to these findings; mass loss (after 406 days of incubation) of *Betula* increased from 16.1% to 26.2% when decomposing in combination with *Sphagnum*, and *Sphagnum* decomposed even slower in combination with *Betula* litter (from 4.7% to 1.9%).

Our results indicate that the change in litter quality rather than its effects on microclimate is the main way in which vascular litter inputs alter the role of Collembola in carbon turnover. Collembola are plastic in their diet choice, which implies that changes in carbon turnover rates in situations where vegetation shifts occur, might well be due to diet shifts of the present decomposer community rather than by changes in species composition.

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1. Introduction

Understanding and predicting effects of climate change on ecosystem processes is an urgent challenge for ecologists. One major difficulty is that climate change not only influences ecosystem processes directly through temperature rise and changed precipitation regimes, but also indirectly by its effects on plant and animal communities (Wookey et al., 2009; Kardol et al., 2010). These latter effects are especially apparent in high-latitude and temperate alpine ecosystems, where shifts toward dominance of shrubs and trees over existing moss communities due to climate

change have been predicted and observed (Sturm et al., 2001; Chapin et al., 2005; Elmendorf et al., 2012a,b). Through subsequent ecosystem feedbacks and cascade processes (Wookey et al., 2009), changes in vegetation composition can alter patterns of growth, allocation and nutrient uptake by the vegetation. In turn this will affect dead organic matter quantity and quality and, thereby, the soil decomposer community and decomposition rates (Gogo et al., 2011). Soil invertebrates, a key group of litter decomposers and microbivores in these ecosystems, are expected to respond strongly to changes in plant dominance (Bardgett and Wardle, 2010), which might have large consequences for organic matter breakdown (Laiho et al., 2001) and, thereby, soil carbon dynamics.

One important pathway by which altered plant cover and composition cascade down to the soil invertebrate community is by

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litter input to the soil ecosystem (Bardgett and Wardle, 2010). Increases in 'shrubbiness' (Wookey et al., 2009) of moss dominated high-latitude ecosystems will alter the quality and quantity of litter input (Cornelissen et al., 2007), which might, subsequently, change the soil invertebrate community composition and the spatial patterning of component species (Hättenschwiler et al., 2005; Berg, 2012). Chemical properties of litter may not only affect the soil invertebrate community directly, but also indirectly through its effects on the microbial community, which is considered to be one of their main food sources (Hogervorst et al., 2003; Chahartaghi et al., 2005). Since soil invertebrate species select food sources of higher quality if they can (Ponge, 2000; Schneider and Maraun, 2005), input of litter with higher quality could lead to changes in spatial patterning of soil invertebrate species density and composition, both horizontally and vertically (Berg and Bengtsson, 2007). This, in turn, may feedback on the breakdown of this litter.

Additionally, a change in the physical properties of litter might structure soil invertebrate communities by altering the local microclimate (Coulson et al., 1993; Hättenschwiler et al., 2005) to which soil invertebrates are very sensitive (Huhta and Hanninen, 2001). Changes in these conditions over space and/or time lead to spatial patterning of soil invertebrates (Faber and Joosse, 1993; Berg et al., 1998; Briones et al., 2007) and shifts in species composition (Makkonen et al., 2011). Knowledge about the importance of variation in the physical aspects of litter relative to chemical quality is important for understanding and predicting its effects on the decomposer community, since species differ in their sensitivities to alterations in microclimate vs the quality of their food (Krab et al., 2010).

The consequences of shifts in the soil invertebrate community structure might affect decomposition rates, since soil invertebrates are functionally dissimilar in their preferences and activities with respect to consumption of both litter and litter-dwelling microbes (Faber and Verhoef, 1991; Setälä et al., 1998; Heemsbergen et al., 2004; Vos et al., 2011). Spatially, invertebrates have specific effects on the decomposition process of different litter species (horizontal patterning) and in subsequent strata of a given litter species (vertical patterning). In shallow fresh litter layers of temperate pine forests, for instance, the activities of soil invertebrates are known to immobilize nutrients. However, soil invertebrates mobilize nutrients deeper in this soil profile, where older fragmented pine litter is located (Faber, 1991). Shifts in spatial patterning or in species composition, therefore might have direct consequences for organic matter breakdown and related carbon fluxes (Briones et al., 2007).

Despite the importance of the above-mentioned processes, there are to our knowledge no integrated studies that have investigated the role of changing litter inputs for the soil food web and carbon processing in high-latitude bog ecosystems. In these ecosystems, Collembola are particularly ubiquitous microarthropod decomposers and microbivores. The aims of the present study were therefore to investigate (1) the role of soil invertebrate (Collembola) species composition in organic matter processing in a subarctic bryophyte dominated peatland, and (2) how vascular plant litter input in these peatlands impacted on Collembola abundance, diversity and litter carbon processing contributions. By using a stable ^{13}C isotope tracer approach we investigated the relative contributions of moss vs vascular plant leaf litter to the fine scale vertical spatial distribution and nutrition of Collembola species. We have used carbon isotopes, firstly, because carbon is the key element of interest for peatland climate feedback (Gorham, 1991; Dorrepaal et al., 2009) and, secondly, since the $\delta^{13}\text{C}$ signal of diet propagates with very little fractionation (less than 1‰) into consumers (Deniro and Epstein, 1978), this allows distinction between the food sources with different ^{13}C signatures (Fry, 2006). Through addition of ^{13}C enriched vascular plant litter to a non-enriched peat system, and

vice versa, we studied how Collembola communities responded to changes in litter input by analyzing their diversity, abundance, diet choice ($\delta^{13}\text{C}$ signature), and species-specific responses to leaf litter composition. If chemical properties of litter dominate the response of the soil invertebrate community we hypothesize there to be shifts in diet choice of Collembola, and thus in their $\delta^{13}\text{C}$ values. These shifts then may be either a direct effect of changes in litter quality (when Collembola act as detritivores) or an indirect effect, through litter quality induced changes in the microbial community (when Collembola act as fungivores or microbivores). If microclimate is the dominant driver, we do not expect diet shifts, but rather changes in Collembola species abundances when leaf litter composition changes. We also hypothesize that individual species differ in their response to vascular plant litter input with respect to chemical vs microclimatic aspects. We will finally try to link the carbon processing properties of the (changing) Collembola communities to mass loss patterns of mosses and/or vascular plant litter.

2. Methods

2.1. Study site

The experiment was carried out in Abisko, North Sweden (68° 21'N, 18°49'E, 340–370 m above mean sea level) from June 2009 until August 2010, preceded by plant ^{13}C labeling in 2008. Precipitation in this area is low, on average 320 mm per year, and average monthly temperatures vary generally between $-15\text{ }^{\circ}\text{C}$ (February) and $15\text{ }^{\circ}\text{C}$ (July) with a winter mean of $-6\text{ }^{\circ}\text{C}$ and a summer mean of $7\text{ }^{\circ}\text{C}$. The growing season lasts about 130 days (Krab et al., 2010). The location of the experiment was on a blanket bog on a bank of Lake Torneträsk near the Abisko Research Station. This bog is dominated by the moss *Sphagnum fuscum* (Schimp.) H. Klinggr., vascular plants have a cover of about 25%, mainly consisting of *Empetrum hermaphroditum* Hagerup, *Betula nana* L., *Vaccinium microcarpum* L., *Vaccinium uliginosum* L., *Rubus chamaemorus* L., *Eriophorum vaginatum* L., and *Calamagrostis lapponica* (Wahlenb.) Hartm. (Aerts et al., 2009). This bog was surrounded by forest dominated by *Betula pubescens* Ehrh.

2.2. Isotope labeling of moss and leaf litter

In the summer of 2008, litter of *S. fuscum* (Schimp.) H. Klinggr. and *B. pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman (from here on referred to as '*Sphagnum*' and '*Betula*') was labeled by sequential pulse labeling of the living plants with ^{13}C enriched CO_2 . For *Sphagnum*, green parts of vascular plants were mechanically removed from a plot of 1 m^2 preceding the labeling. To enrich the plant material we dissolved labeled sodium bicarbonate (99%) in sulfuric acid (2 M) creating 400 ppm of $^{13}\text{CO}_2$. This $^{13}\text{CO}_2$ was added to the headspace of a transparent chamber that covered the 1 m^2 plot completely (0.2 m^3). We conducted 13 labeling sessions, which each lasted for 12 h. At the start of the experiment, the labeled *Sphagnum* core contained one layer of isotopically enriched moss. This layer consisted out of last years freshly grown moss; this resulted in an enrichment located in the two top centimeter of the core (Table S1).

Five *Betula* trees (2 m height) were enriched by adding $^{13}\text{CO}_2$ to the air trapped by a closed plastic bag ($2 \times 2\text{ m}$) that was placed over the canopy and wrapped airtight around the tree trunk. *Betula* trees received 5 pulse-labeling sessions that lasted 20 h. After the final pulse-labeling session, a net was wrapped around the tree trunk to collect the senesced leaf litter.

A minimum interval of 24 h between all labeling sessions let the plants recover from coverage. The labeling resulted in an average

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